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European (22.9 mm), Tornewton Cave, England (Illinoian; 21.0 mm), and European Cromerian (20.0 mm) wolverines. In comparison, the Old Crow mandibles have M_1 s with a mean length of 19.8 mm – smaller than any of Kurtén's samples and closest in size to the Cromerian specimens. As I suspect that the Old Crow mandibles are of Sangamon age (or earlier), according to evidence from Old Crow Locality 44, I suggest that the reduction in size of the teeth may reflect that to be expected in an interglacial period (see, for example, Kurtén 1973, p. 5), rather than indicating close affinities with European wolverines of much earlier (Cromerian) Pleistocene age.

The earliest evidence of the wolverine is the small *Gulo schlosseri* from Günz (?Nebraskan) deposits of Episcopia on Cyprus. According to Kurtén (1968, p. 92), it probably arose from *Plesiogulo*, a less specialized ancestor that lived in Eurasia and North America during the Pliocene. However, Korotkevich and Semenov (1975, p. 38) state that *Plesiogulo crassa* cannot be a direct ancestor of *Gulo* because its dentition shows specialization in a different direction. *Gulo schlosseri* may have been adapted to a warmer environment than are living wolverines, and perhaps the boreal adaptation of the genus did not begin until the Mindel (?Kansan) glaciation when *Gulo gulo*

appears at Mosbach, West Germany and Choukoutien, China (Kurtén 1968, pp. 90-93).

Apparently wolverines entered North America during the Kansan glaciation, for specimens from Port Kennedy Cave, Pennsylvania and Cumberland Cave, Maryland are considered to be of that age (E. Anderson, personal communication 1975). This raises the possibility that there was a Holarctic population of *Gulo schlosseri* during Kansan time, from which *Gulo gulo* may have evolved in both Eurasia and North America almost simultaneously, facilitated by genetic contact across Beringia (B. Kurtén, personal communication 1976). A few fossils of Wisconsin age are known from Little Box Elder and Jaguar caves in Wyoming and Idaho, respectively. Two fairly large samples have been collected at late Wisconsin or early postglacial sites; Animal Trap in Colorado, and Moonshiner Cave, Idaho (Kurtén and Anderson 1972, p. 33). The Old Crow specimens constitute the first Pleistocene records of wolverine for Canada. Although wolverine fossils probably have been found in Alaska (Geist 1953, p. 173; see chart in Guthrie 1972), to my knowledge, they have not been described.

The living North American wolverine (*Gulo gulo luscus*) is conspecific with the Eurasian animal (*Gulo gulo gulo*)

(Kurtén and Rausch 1959, p. 19). Thus, the species is a member of the Holarctic fauna and ranges from Scandinavia through northern Asia to northern North America. North American wolverines are not specialized in their habits, and frequent boreal forest, tundra and alpine tundra regions. The young are born in dens. Wolverines feed mainly on birds and mammals, such as ground squirrels, marmots and beavers, but occasionally they attack caribou, moose, deer and mountain goats. They are primarily scavengers and often follow migrating caribou herds, cleaning up carcasses left by wolves and bears, and crushing the bones with their powerful carnassial teeth.

Taxidea taxus (American badger)

Fossils of the badger (Figures 43A-D, Tables 44-45) are rare in Yukon Pleistocene deposits. Only two specimens are known, and both are from the Dawson Area.

Referred specimens

NMC 17260 from Dawson Locality 28 is a cranium with RP^3-RM^1 (RP^3 is badly damaged and the posterior margin of RP^4 is missing), LP^3-LM^1 (only the roots of LP^3 and LP^4 are preserved), and alveoli for the remaining teeth. The right auditory bulla is damaged, the posterior half of



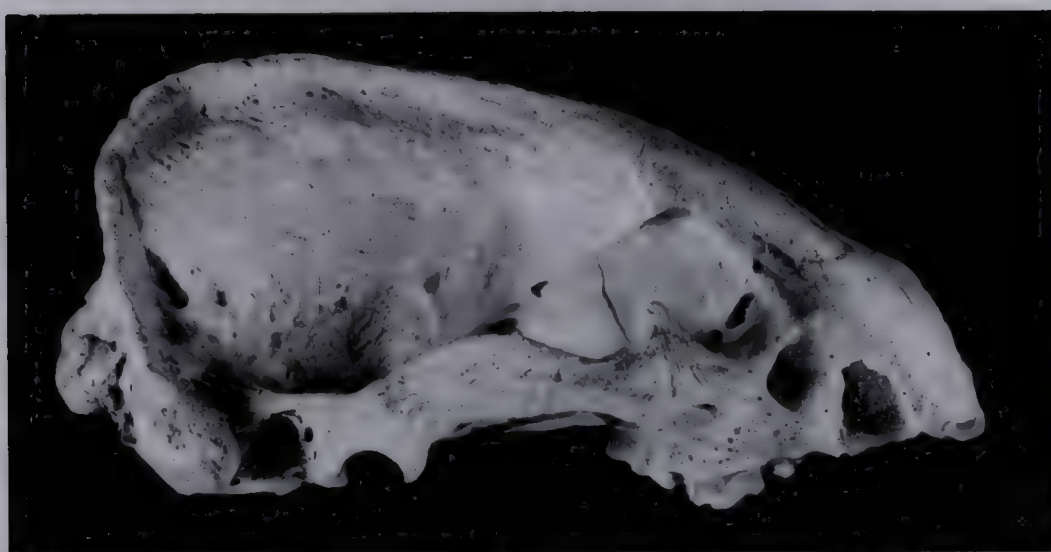
Figure 43. Cranium (NMC 17260, Dawson Locality 28)
of a Pleistocene American badger (*Taxidea
taxus*).

A. Dorsal view. B. Right lateral view.
C. Ventral view.

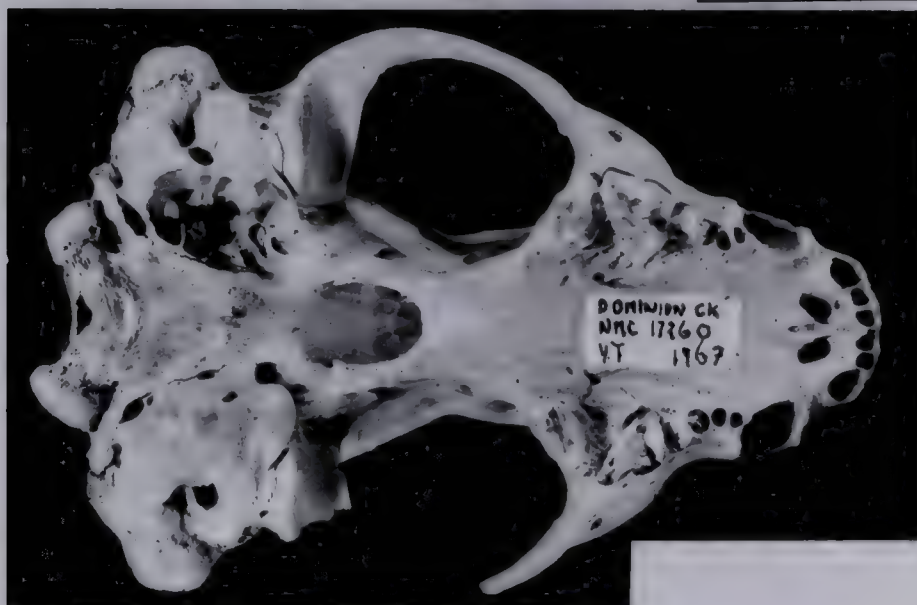
D. Anterior view of a right humerus (NMC
13486, Dawson Locality 32) of a Pleistocene
American badger (*Taxidea taxus*).



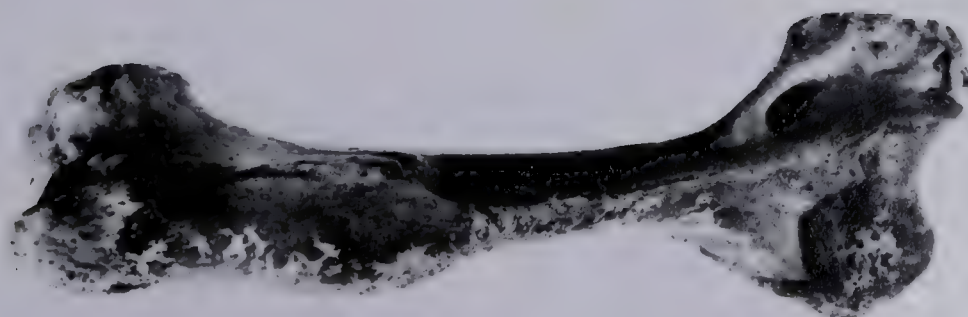
A



B



C



D

Table 44. Measurements of a Pleistocene American badger (*Taxidea taxus*) cranium from the Yukon Territory compared to crania of Recent American badgers from Canada, and Pleistocene and Recent American badgers from the United States.

Specimens	Sex	Measurements (mm)*												
		1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Taxidea taxus</i> . Pleistocene, Y.T.														
NMC 17260 Dawson Loc. 28	-	134.5 [†]	121.2	95.4e	86.3	34.3	29.6	72.3	48.3	12.1	11.0	10.2	11.6	43.6
<i>Taxidea taxus</i> . Recent, Canada														
NMC 8086 Alberta	♂	130.0	116.0	98.9	82.2	29.4	29.2	68.1	44.9	12.2	10.6	11.2	10.1	43.4
NMC 8026 Alberta	♀	123.7	111.1	79.4	74.7	27.2	27.6	64.6	40.5	11.2	9.8	9.8	9.6	39.1
NMC 10712 B.C.	♀	130.9	117.8	86.7	81.2	32.2	30.5	69.8	43.6	11.9	10.3	11.2	11.0	43.1
NMC 10603 B.C.	♂	129.6	116.3	87.1	81.1	31.3	31.8	68.2	45.3	12.3	10.7	12.1	10.9	42.2
NMC 10609 B.C.	♂	126.0	114.6	82.7	85.4	29.4	29.3	67.3	41.6	12.5	11.0	12.3	10.6	43.1
NMC 10104 B.C.	?♀	128.1	116.6	81.6	81.2	31.2	29.8	67.9	41.9	12.4	10.5	11.2	11.0	43.4
<i>Taxidea taxus</i> . Pleistocene, U.S.A. (Anderson 1968, p. 40, Table 17) Little Box Elder Cave, Wyoming														
M	-	-	-	-	-	-	-	-	-	11.8	10.4	11.1	10.3	39.9
OR	143.3	128.2	94.4	91.2	31.3	-	-	70.8	47.9	11.4-	9.7-	10.3-	9.4-	38.8-
N	1	1	1	1	1	-	-	1	1	7	8	9	9	7
<i>Taxidea taxus</i> . Recent, U.S.A. (Anderson 1968, p. 40, Table 17) Colorado														
M	121.3	110.4	76.7	75.3	24.5	-	-	61.2	41.8	11.8	10.5	12.1	10.3	39.8
OR	113.6-	103.6-	69.3-	70.7-	27.6-	-	-	58.9-	39.9-	10.5-	9.5-	9.9-	9.6-	33.4-
N	129.7	118.4	86.6	87.7	29.3	-	-	65.6	43.6	12.8	12.4	12.5	11.9	40.0
	12	12	14	13	14	-	-	14	14	14	14	14	14	14
<i>Taxidea taxus</i> . Recent, U.S.A. (Arizona) (Anderson 1968, p. 40, Table 17)														
M	120.9	-	76.9	73.5	31.2	-	-	53.6	37.9	11.6	9.7	10.4	10.2	40.0
OR	115.8-	-	72.8-	70.0-	28.9-	-	-	57.3-	36.8-	10.9-	9.5-	9.7-	9.6-	38.7-
	123.9		79.4	76.7	33.1			60.4	39.1	13.1	10.1	12.2	11.3	40.9
N	3	3	3	3	3	-	-	3	3	3	3	3	3	3

* 1 - Total length.

2 - Zygomatic length (posterior margins of alveoli for upper incisors to lower border of foramen magnum).

3 - Zygomatic breadth.

4 - Mastoid breadth.

5 - Interorbital breadth.

6 - Postorbital constriction.

7 - Palatal length.

8 - Palatal width across P⁴s.

9 - P⁴ length.

10 - P⁴ width.

11 - M¹ length.

12 - M¹ width.

13 - Alveolar length C¹-M¹.

Table 45. Measurements of a Pleistocene American badger (*Taxidea taxus*) humerus from the Yukon Territory compared to humeri of Recent American badgers from Canada.

Specimens	Sex	Measurements (mm)*							
		1	2	3	4	5	6	7	8
<i>Taxidea taxus</i> .Pleistocene Y.T.									
NMC 13486 Dawson Loc. 32	-	109.2	25.4	29.1	9.1	12.7	34.5	15.6	3.1
<i>Taxidea taxus</i> .Recent, Canada									
NMC 9992	-	107.8	24.2	27.4	9.8	10.8	33.9	16.2	3.3
NMC 28358	-	108.1	25.0	27.0	9.1	11.1	31.9	15.8	2.6
NMC 3121	♀	97.8	22.2	24.3	8.7	12.0	31.5	14.6	2.5
NMC 32137	♀	89.3	21.4	22.5	7.6	9.5	28.6	13.7	2.3
NMC 32138 immature	♂	87.8	22.3	22.9	8.2	10.2	28.5	13.3	2.9
NMC 32139 immature	-	84.7	19.7	21.9	6.9	8.5	27.2	12.5	3.2

* 1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Minimum shaft width.

5 - Minimum shaft depth above the lateral condyloid crest.

6 - Distal width.

7 - Distal depth.

8 - Minimum anteroposterior diameter of shaft enclosing entepicondylar foramen.

the left zygomatic arch is lacking, and bone has been eroded away forming large cavities in the ventrolateral regions of the occiput. The occipital condyles are also heavily eroded. Sutures are well fused, the teeth are heavily worn, and the sagittal and lambdoidal crests are well developed, suggesting that an old individual is represented. NMC 17260 is similar in size (slightly shorter, but broader) to a late Wisconsin cranium (UCM 21928) from Little Box Elder Cave, Wyoming, which is larger than any specimens Anderson (1968, p. 39) had examined or seen reference to in the literature. It is larger in most dimensions, except P^4 and M^1 length, than Recent American badger crania from Alberta and British Columbia to which it was compared. The bone is tan in color like that of NMC 13486.

NMC 13486 from Dawson Locality 32 is a right humerus that is complete except for part of the lateral condyloid crest. Its total length and general robustness suggest that it represents an adult male. Of Recent specimens to which it was compared, the fossil most closely resembles a specimen of *Taxidea taxus jeffersoni* from Yahk, British Columbia (NMC 9992). This fossil constitutes the first record of a badger from the Yukon Territory (Harrington and Clulow 1973, p. 700). The specimen is

manila in color and has rootlet impressions over much of its lateral surface, as if it had been deposited in a grassland. *Bison crassicornis* and mammoth (*Mammuthus* sp.) bone from deposits at this locality yielded radiocarbon dates of $22,000 \pm 1,400$ years B.P. (I-3570) and $32,350 \pm 1,750$ years B.P. (I-4226), respectively. Presumably this specimen is of late Wisconsin age.

Discussion

Badger fossils from the Dawson region are probably of Wisconsin age. Their rarity suggests that suitable grassland habitat was confined in area or available to badgers for a relatively short time, or both. Evidently this species did not reach as far north as the Old Crow Basin - perhaps because of more severe permafrost conditions. Badgers did penetrate as far northwest as the Fairbanks region of Alaska however, for Geist orally reported their presence in Pleistocene deposits there to Péwé (1975a, p. 97). Hibbard (Skinner *et al.* 1972, p. 110) mentions examining seven badger skulls from late Pleistocene deposits of Alaska. In southern Canada, the badger (*Taxidea* sp.) has been reported from a Sangamon interglacial fauna at Fort Qu'Appelle, Saskatchewan (Khan 1970, p. 13) and probably from Wisconsin interstadial or Sangamon deposits at Saskatoon, Saskatchewan (Harrington 1976 MS. p. 25).

According to Thenius and Hofer (1960, p. 165), *Melodon* from the upper Miocene to lower Pliocene of Asia and *Parataxidea* from the lower Pliocene of Eurasia are nearest the origins of both European (*Meles*) and American (*Taxidea*) badgers. *Taxidea* sp. and *Taxidea* cf. *taxus*, from the upper Pliocene Hagerman and Rexroad faunas of Idaho and Kansas respectively, are the earliest badgers known from North America, implying movements of an ancestral stock across the Bering Isthmus from Asia to North America prior to the reopening of the seaway in late Pliocene time (Hopkins 1967, p. 458). *Taxidea* has also been reported from the earliest Pleistocene (late Blancan) faunas of Cita Canyon, Texas; Deer Park, Kansas; and Broadwater and Sand Draw, Nebraska (Skinner *et al.* 1972, p. 128).

Badger remains are known from several early and middle Pleistocene localities in the eastern United States, including Cumberland Cave, Maryland (Gidley and Gazin 1938) and Port Kennedy Cave, Pennsylvania, which now appear to be of Kansan age (E. Anderson, personal communication 1976). Remains of *Taxidea taxus* are also common in many Wisconsin localities in the United States such as: Little Box Elder Cave, Wyoming; Jones Ranch, Kansas; Isleta Caves and Burnet Cave, New Mexico;

Papago Springs and Ventana Cave, Arizona; Schuiling Cave, Rancho La Brea, Carpenteria, McKittrick and Potter Creek Cave, California (Anderson 1968, p. 40).

The unusual degree of variability in qualitative characteristics, such as the number of cusps on M_1 , M^1 and P^4 , even within a single population of one subspecies, makes definition of new species and subspecies of *Taxidea* difficult. A single living species, *Taxidea taxus*, is recognized.

Badgers of the genus *Taxidea* are confined to North America, ranging from southwestern Canada to central Mexico - west of the Mississippi, except in the Great Lakes region. Pleistocene records from the Dawson Area are therefore some 1,200 miles (1,930 km) northwest of the present limits of *Taxidea taxus* in Alberta. I think large stretches of grassland or parkland must have existed between the prairies and Dawson and Fairbanks during the late Pleistocene in order to explain the presence of badger fossils in the latter areas.

Badgers are relatively large members of the weasel family with stout, dorsoventrally flattened bodies and short legs. Their foreclaws are strongly developed for digging. Females are about 10% smaller than males.

Badgers occupy open prairies and parklands. They are good paleoenvironmental indicators of grasslands; in this respect it is worth referring again to apparent grass rootlet impressions on the surface of the fossil humerus NMC 13486. Badgers are primarily fossorial and nocturnal animals that tend to hibernate during the winter months, particularly in the northern parts of their range (which would have been advantageous to survival in the Yukon Territory during the late Pleistocene). Badgers live in grassy nests set in chambers at the ends of burrows. They often enlarge ground squirrel and prairie dog burrows for their own use. Their diet consists mainly of ground squirrels, pocket gophers, prairie dogs and other animals such as mice, voles, ground nesting birds and insects. Presumably arctic ground squirrels (*Spermophilus parryi*) would have been their basic prey in the late Pleistocene of the Yukon. The American badger seems to have few predators.

Spilogale sp. (spotted skunk)

A single specimen of the spotted skunk (Figure 44A-C, Table 46) has been collected from the Pleistocene deposits of the Yukon Territory. It constitutes the first record of the species from Eastern Beringia, and is of



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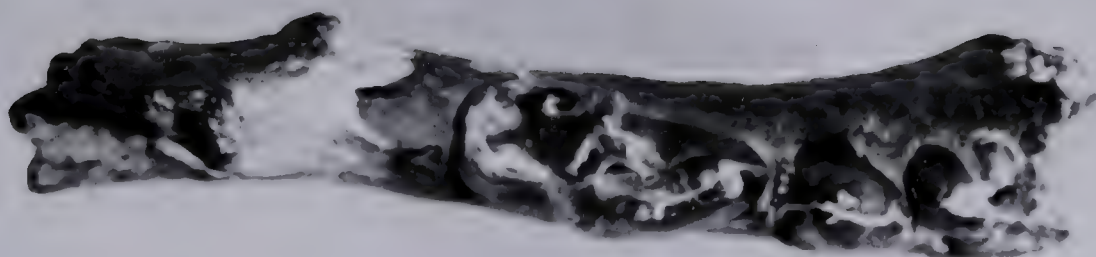


Figure 44. Right mandible with RP_2 - RM_1 (NMC 25529, Old Crow Locality 44) of a Pleistocene spotted skunk (*Spilogale* sp.).

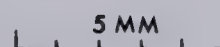
- A. Lateral view.
- B. Occlusal view.
- C. Medial view.



A



B



C

Table 46. Measurements of a Pleistocene spotted skunk (*Spilogale* sp.) mandible from the Yukon Territory compared to mandibles of Recent spotted skunks (*Spilogale gracilis*) from British Columbia and Recent striped skunks (*Mephitis mephitis*) from Alberta.

Specimens	Sex	Measurements (mm)*							
		1	2	3	4	5	6	7	8
<i>Spilogale</i> sp. Pleistocene, Y.T.									
NMC 25529 Old Crow Loc. 44	-	6.8	3.7	8.8	7.9	3.4	4.9	2.9	16.8
<i>Spilogale gracilis</i> .Recent, B.C.									
NMC 29260	♂	4.3	3.2	6.6	7.9	3.5	4.9	3.1	15.4
NMC 873	♂	5.9	3.5	6.7	7.9	3.8e	4.4	3.5	16.8
NMC 851	-	4.4	3.2	6.1	7.8	3.5	4.6	3.4	16.0
NMC 883	♂	5.0	3.2	5.9	7.9	3.4	4.4	2.8	15.3
NMC 823	♂	4.6	3.0	5.9	8.0	3.3	4.5	3.2	15.6
NMC 822	♀	6.0	3.0	5.9	7.6	3.1	4.2	2.9	15.6
<i>Mephitis mephitis</i> .Recent, Alta.									
NMC "69"	-	7.8	4.9	9.3	10.3	5.0	6.3	4.9	22.9
NMC 18494	♂	6.8	4.2	8.2	10.2	5.0	5.8	4.9	21.6
NMC 18478	♀	8.5	4.5	9.4	10.0	4.7	5.6	4.7	21.4
NMC 18502	-	9.7	5.4	9.2	10.7	5.0	5.7	5.0	20.8
NMC 18480 (immature)	♀	5.9	4.3	7.6	9.3	4.9	5.6	4.7	19.8
NMC 18501	-	7.3	4.0	7.5	9.9	4.9	5.2	4.8	19.0

* 1 - Mandible depth below centre of M_1 .

2 - Mandible width at centre of M_1 .

3 - Mandible depth below centre of P_3 .

4 - M_1 length.

5 - M_1 width.

6 - Length M_1 trigonid.

7 - Width M_1 talonid.

8 - Alveolar length P_3 - M_2 .

particular interest because it is known to be more than 54,000 years old - possibly of Sangamon interglacial age. In the present interglacial, spotted skunks are found only far south of the Yukon.

Referred specimen

NMC 25529 from Old Crow Locality 44 is a right mandible with RP_2 - RM_1 and the alveolus for RM_2 . The anterior of RP_3 is damaged, and this region is difficult to interpret. Apparently alveoli for RP_2 (one filled by a partial root) lie immediately anterior to RP_3 and behind the posterior portion of the socket for the vertically rising canine. The trigonid of M_1 shows signs of heavy wear: evidently an old individual is represented. The shape and proportions of the teeth and the size of the mandible are indicative of a skunk smaller than the striped skunk (*Mephitis mephitis*). Of the comparative Recent skunk material at hand, NMC 25529 is closest to *Spilogale*, and it is referred to *Spilogale* sp. until further comparative material becomes available and a specific designation can be given. The fossil mandible falls within the range for *Spilogale gracilis* in all dimensions measured except in depth and width of the mandible at M_1 and depth of the mandible below P_3 . In addition to the robustness of the mandible, the specimen is notable for the trenchancy of RP_4 , despite

wear on its tip, and the general straightness of the inferior profile of the mandible. Both are characteristic of *Spilogale*. Mental foramina of the fossil are located below P_3 and P_4 , as in *Spilogale*, and the degree of dental crowding seen in NMC 25529 is characteristic of *Spilogale*. A natural size line illustration of a male *Spilogale putorius interrupta* (KU 14237) (Hall and Kelson 1959, p. 929, Figure 496) is closer in appearance to NMC 25529 than any recent specimens of *Spilogale gracilis* that I have examined. KU 14237 has a thicker anterior mandible like the Old Crow fossil because of a downward deflection of the jaw at the symphysis.

Discussion

It is interesting to note that the spotted skunk, now considered by mammalogists to be adapted to relatively warm conditions because of its southerly distribution in North America (Hall and Kelson 1959, p. 930, Map 472) should have reached a position approximately 1,380 miles (2,220 km) north northwest of the northernmost limit of its range in the present interglacial (Alta Lake, 70 miles (113 km) north of Vancouver, British Columbia). This fact does not seem quite so remarkable when the stratigraphic situation of the fossil is considered. It was excavated from the fossiliferous zone at Old Crow Locality 44, and is therefore more than 54,000 years old,

and very likely of Sangamon interglacial age. Frenzel (1973, pp. 132-138) shows that the climate over the Northern Hemisphere during the Sangamon was substantially warmer, and perhaps wetter in places, than at present.

Skunks have not been reported previously from Eastern Beringia. In Canada, a specimen of the spotted skunk, *Spilogale* cf. *putorius*, is known from an early mid-Wisconsin fauna at Medicine Hat, Alberta (C.S. Churcher, personal communication 1974). Most of the other mammals belonging to this fauna suggest a prairie grassland habitat (Harrington 1976 MS. p. 37). There are no other Canadian Pleistocene records.

The skunks (Mephitinae), presently found only in the New World, are closely allied to the badgers, but their teeth are better adapted to grinding than shearing and they are less carnivorous than badgers. *Mioemephitis*, from the early Miocene of Europe, is the geologically earliest skunk recognized. *Promephitis*, of the Eurasian Pliocene, is closer to the ancestral stock of the living skunks.

Probably the ancestors of the spotted skunk

entered North America via the Bering Isthmus about middle Pliocene time with the ancestors of the American badger. *Spilogale rexroadi*, from the upper Pliocene (early Blancan) Rexroad fauna of Kansas, seems to be the first representative of the genus in North America. It is worth mentioning two other genera that have broad affinities with *Spilogale*. *Buisnictis*, a small, short-faced skunk that lived in western North America from middle Pliocene to early Pleistocene time, probably had similar habits to *Spilogale*. *Buisnictis burrowsi*, from the earliest Pleistocene of Nebraska, had the anterior deepening of the mandible seen in NMC 25529, but differs from *Spilogale* in its larger size, straighter inferior margin of the mandible and more sectorial teeth (Skinner *et al.* 1972, pp. 110-128). *Brachyprotoma pristina*, a small, extinct, short-faced skunk that apparently survived until Illinoian time in the Appalachians (Guilday 1971, p. 237), also has similar features to *Spilogale*. A detailed study of the affinities of these three genera is required.

Among other faunas of later Pleistocene age that have produced *Spilogale* remains are: the Borchers fauna, Kansas (Aftonian interglacial); Inglis IA (early Yarmouth interglacial); faunas of the Appalachian region and

Coleman IIA, Florida (Illinoian); Slaton, Texas, Cragin Quarry, Kansas, Reddick IA, Florida (Sangamon interglacial); and the following faunas of Wisconsin age: various faunas in Texas; Jones Ranch, Kansas; Papago Springs, Arizona; Jaguar Cave, Idaho; McKittrick, Carpinteria, Rancho La Brea, Potter Creek Cave in California; and various faunas in Florida (Hibbard 1958, p. 19; Hibbard 1970; Guilday 1971, p. 237; Kurten and Anderson 1972, pp. 33-34; Webb 1974, Table 2.1).

The spotted skunk presently occurs from southern Central America to southern North America. Although most workers consider that *Spilogale* is monotypic, Hall and Kelson (1959, p. 930) recognize four nominal species. Of these, *Spilogale gracilis* penetrates northward to extreme southwestern coastal British Columbia, and *Spilogale putorius* approaches the southern Manitoba - Ontario border area. Spotted skunks are smaller and more agile than the striped skunk (*Mephitis*). They are excellent climbers and strictly nocturnal. Families stay together and often hibernate in community dens. For dens, they may usurp woodchuck burrows or use hollow logs or trees or any place that is dark and dry. They are not true hibernators, but several will bed together during severe winter weather. Presumably this adaption in

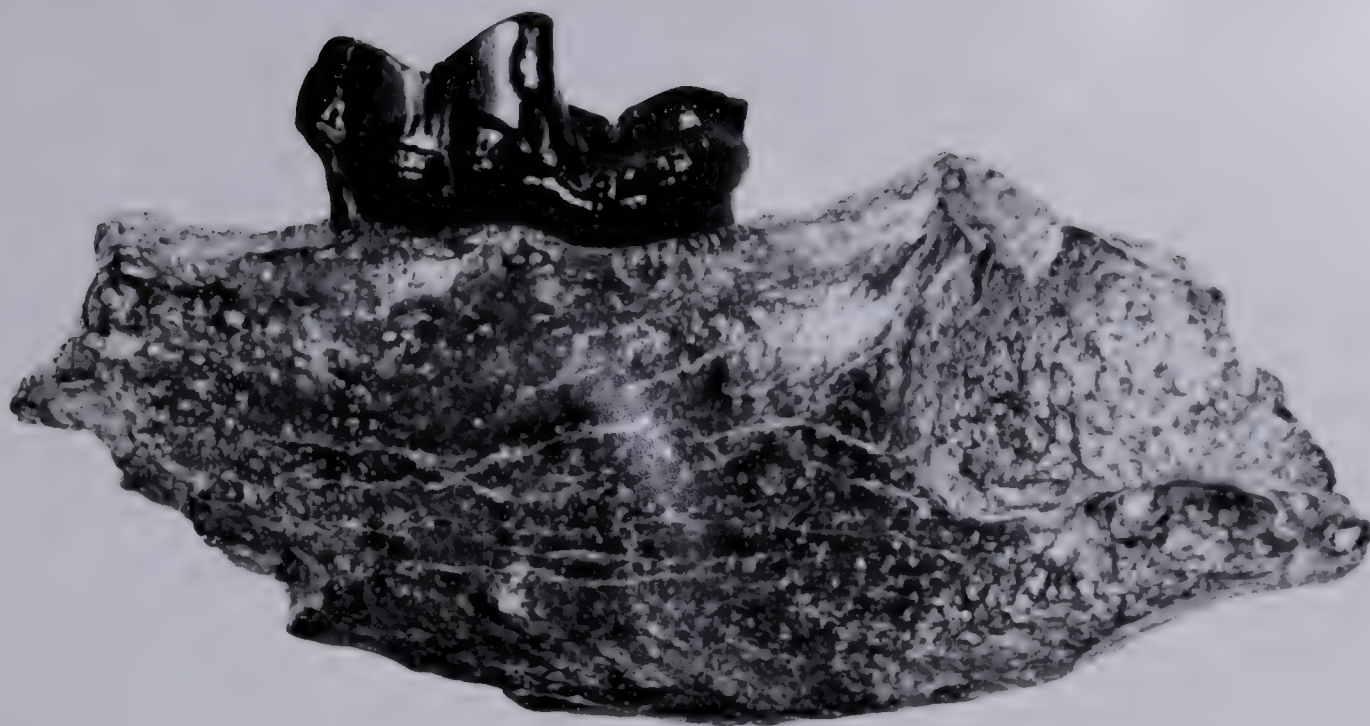
social behavior may have allowed them to survive beyond the Arctic Circle in the Yukon during the late Pleistocene. Spotted skunks are found in a variety of habitats including scrubland, open woodland areas, rocky outcrops and along streams. In British Columbia, *Spilogale* habitat includes lowland thickets and rock slides (Cowan and Guiguet 1965, p. 327). Mammals such as voles and rabbits are their main winter and spring diet, while insects and plants form the bulk of their summer and autumn diet. Beetles and larvae are favorite foods, and it is worth recalling the abundance of beetle remains found in the same stratigraphic zone as the *Spilogale* fossil at Old Crow Locality 44. Birds and bird eggs are also eaten. Their most dangerous predator is the Great Horned Owl. The skunk's defensive scent spray is not effective against predatory birds.

Lontra canadensis (Nearctic river otter)

A single specimen of the river otter (Figure 45A-B, Table 47) is known from Pleistocene deposits of the Yukon Territory. It is the first report of this species for Eastern Beringia. I concur with van Zyll de Jong (1972, pp. 1, 82) that the generic name *Lontra* should replace *Lutra* in describing New World river otters.

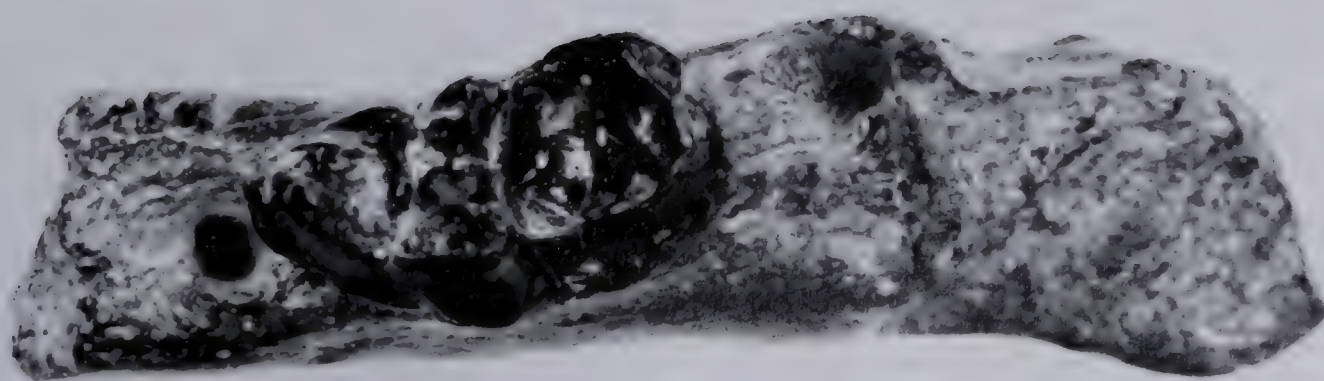
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Figure 45. Left mandibular fragment with LP_4 (NMC 20320, Old Crow Locality 29) of a Pleistocene Nearctic river otter (*Lontra canadensis*).
A. Lateral view. B. Occlusal view.



A

3 CM



B

Table 47. Measurements of a Pleistocene river otter (*Lontra canadensis*) mandible from the Yukon Territory compared to mandibles of Recent river otters from the Yukon Territory and British Columbia.

Specimens	Sex	Measurements (mm)*		
		1	2	3
<i>Lontra canadensis</i> .Pleistocene, Y.T.				
NMC 20329 Old Crow Loc. 29	-	13.2	12.1 ⁺	6.9
<i>Lontra candensis</i> .Recent				
NMC 31814 Y.T.	♂	12.9	14.9	8.3
NMC 33411 Y.T.	♂	11.4	14.8	7.5
NMC 36292 Y.T.	♀	10.5	14.1	7.1
NMC 31744 Y.T.	♂	11.8	13.8	7.8
NMC 29269 B.C.	♀	11.0	15.0	8.3
NMC 29261 B.C.	♂	12.0	14.0	7.3
<i>Lontra canadensis pacifica</i> (= " <i>Lutra canadensis yukonensis</i> "). (van Zyll de Jong 1972, p. 104)				
M	-	-	13.6	7.1
N	-	-	16	16
SD	-	-	0.53	0.39

* 1 - Mandible depth below posterior root of M_1 .

2 - M_1 length.

3 - M_1 width.

Referred specimen

NMC 20320 from Old Crow Locality 29 is a left mandibular fragment with LM_1 , the alveolus for the posterior root of LP_4 and the alveolus for LM_2 . The ascending ramus and bone anterior to LP_4 are lacking. The cusps on LM_1 are well worn; presumably the fossil represents an adult otter. The posterior margin of the LM_1 talonid is missing. The position of the LM_1 cusps exactly match those of Recent *Lontra canadensis*. The relatively deep anterior part of the masseteric fossa extending forward to a point beneath LM_2 , the position of the mandibular foramen, and the posterior rise in the inferior profile of the mandible all fit those characters in Recent river otters. Nor are there remarkable differences in size between the fossil mandible and those of Recent river otters. Therefore, NMC 20320 is referred to *Lontra canadensis*. The bone of the ramus is stained dark brown, whereas the tooth is black.

Discussion

The Yukon fossil appears to be of pre- late Wisconsin age. It seems unusual that Pleistocene otter remains are so rare in the Old Crow Basin, for water and fishes were common there during that period. Despite favorable appearances, perhaps the Old Crow Basin is not good otter habitat, for in travelling much of the

river's length over several years between 1966 and 1975, I have sighted only two of the animals, and they were together. The turbidity of water may be a factor in the local rarity of this species, and their nocturnal habits may militate against their observation by people.

The otters (Lutrinae) evidently originated in Eurasia. *Lutra licenti* from the early Pleistocene of China resembles Recent American river otters in all principle characters, except in its slightly larger size (van Zyll de Jong 1972, p. 73). Otters of this kind make their earliest appearance in North America during the Kansan, suggesting that they crossed the Bering Isthmus about that time. The first record of an otter of the American type from North America is *Lutra rhoadsi* from Port Kennedy Cave, Pennsylvania, which is considered to be of Kansan age. C.G. van Zyll de Jong (1972, p. 79) assumes that *Lutra rhoadsi* is conspecific with *Lontra canadensis* because of their great similarity, and likewise confirms Hall's (1936) opinion that *Lutra parviuspis* from Kansan deposits in Cumberland Cave, Maryland is conspecific with *Lontra canadensis*. A cranium assumed to be of Pleistocene age from Wright County, Iowa and called *Lutra iowa* by Goldman presents a combination of characters linking it with most of the living American species of *Lontra*. Its

species name is best retained. Among other localities, the river otter has been reported from four sites of late Wisconsin age in Florida: Ichetucknee River; Seminole Field; Melbourne; and Vero 2 and 3 (Webb 1974, Table 2.1). One species, *Lontra canadensis*, and seven subspecies of Nearctic river otter are recognized (van Zyll de Jong 1972, p. 81).

The Nearctic river otters occur throughout most of the United States (except the arid southwest), Canada and Alaska (except for most tundra areas). They have long, streamlined bodies, broad flattened heads, and short powerful legs with webbed toes – all excellent adaptations for an amphibious life. Otters prefer to live on shores of deep, clear lakes, rivers, large marshes and ocean bays. They occur rarely in lakes and rivers on the tundra north of the treeline. They are useful paleoenvironmental indicators of the presence of rivers, lakes and fishes. These otters are mainly nocturnal and are active all winter, sheltering only in the most severe weather. They make beds of dried vegetation in hollow logs or usurp dwellings of beavers or muskrats. River otters capture most of their food underwater. Fishes compose the largest part of their diet, but invertebrates, such as stonefly nymphs, water beetles and crayfish are important too. Wolves and

coyotes occasionally kill otters migrating overland. Otherwise they are fairly safe in their aquatic environment.

Family Felidae

Felis (Lynx) canadensis (Canada lynx)

Two specimens of the Canada lynx (Figures 46A-B, Tables 48-49) have been collected from Pleistocene deposits in the Old Crow Basin. These are the first records of this species from ice age sediments in the Yukon Territory.

Referred specimens

NMC 24966 from Old Crow Locality 11A is a left maxillary fragment with LP⁴. The cusps on the tooth are slightly worn, which, in conjunction with the size of the tooth, indicates that an adult lynx is represented. The tooth is slightly larger than those of six Recent lynx from Canada with which it was compared. Of the Recent specimens, it most closely matches NMC 24161, a male from the Yukon Territory. It is markedly smaller than mountain lion (*Felis concolor*) P⁴s seen. Also, the depth from the maxillary-malar suture to the alveolar margin above the paracone of P⁴ in the lynx (and NMC 24966) is approximately 40% of that measurement in the mountain lion. The fossil is stained blackish brown.



Figure 46. Left maxillary fragment with LP⁴ (NMC 24966,
Old Crow Locality 11A) of a Pleistocene
Canada lynx (*Felis (Lynx) canadensis*).
A. Lateral view. B. Occlusal view.

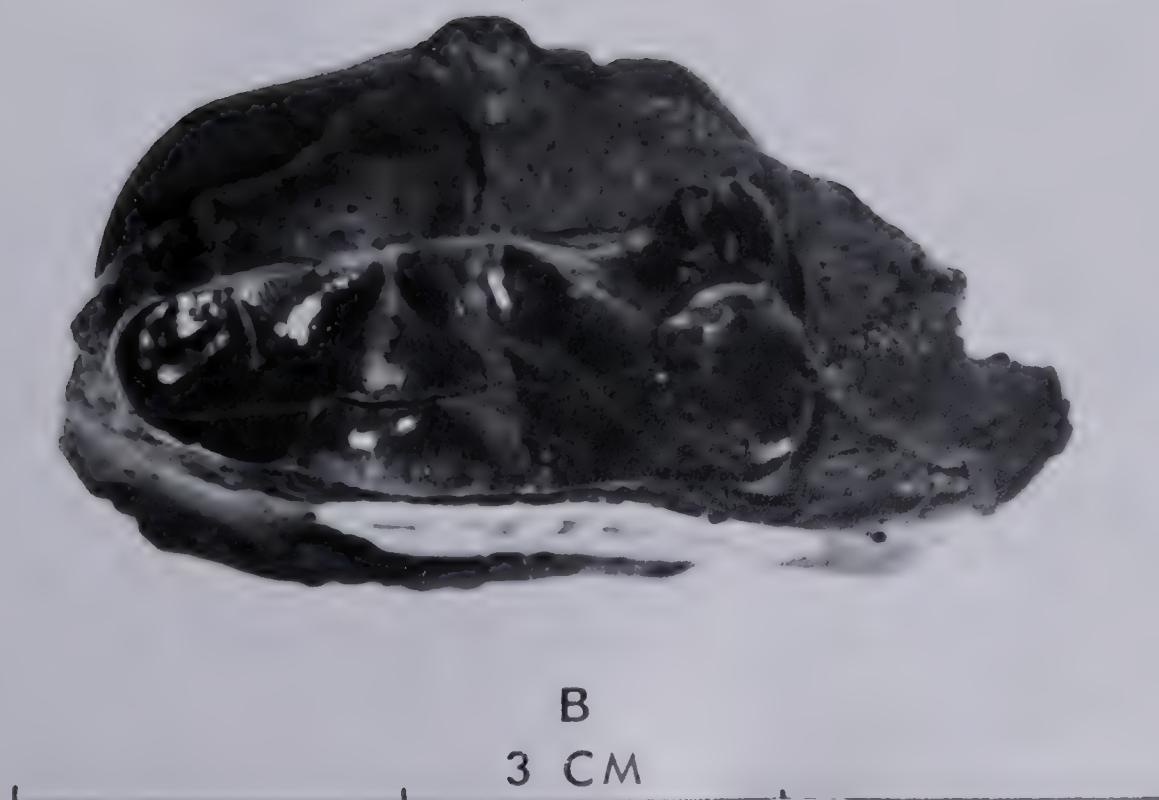
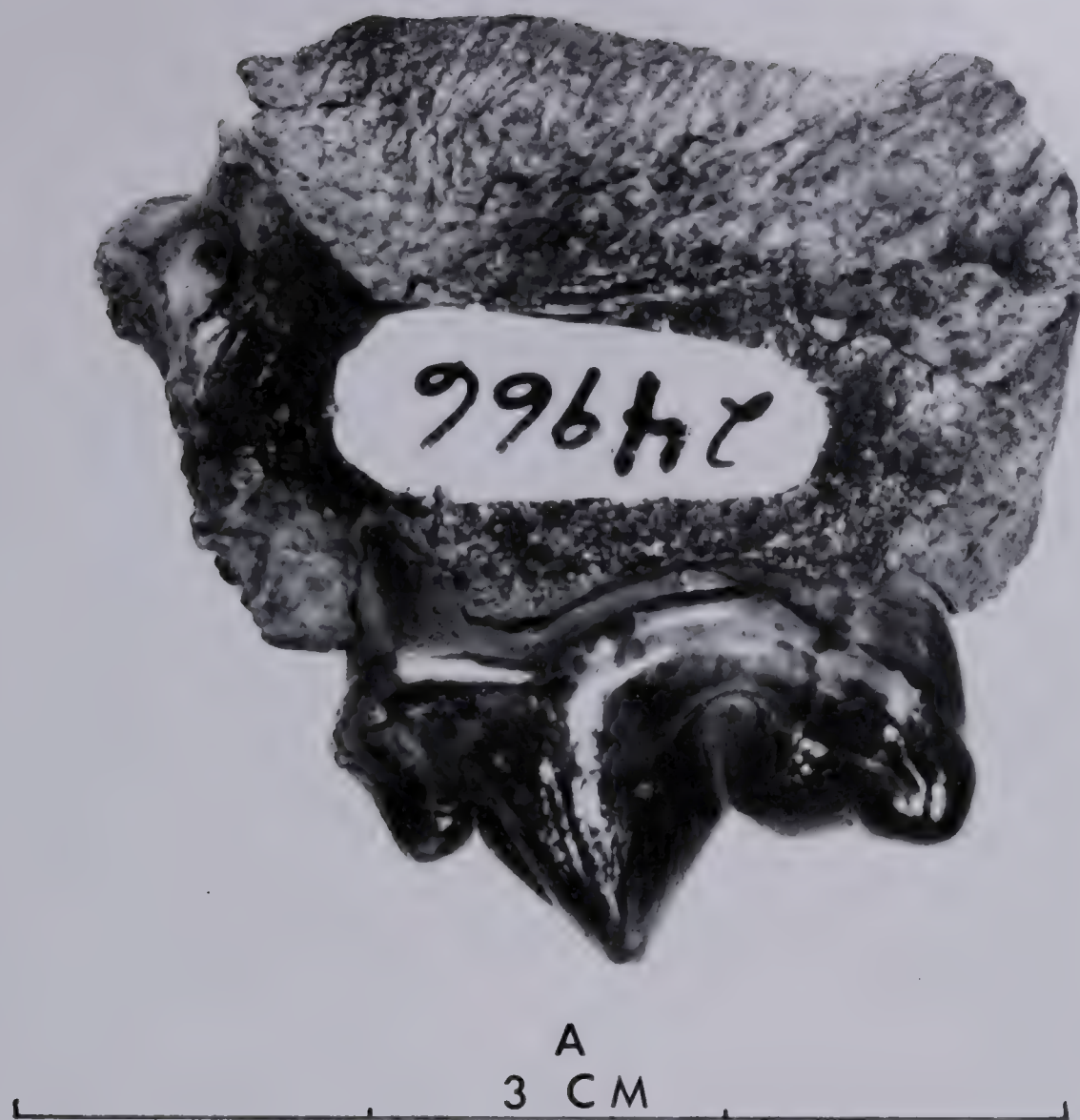


Table 48. Measurements of a Pleistocene lynx (*Felis (Lynx) canadensis*) maxilla from the Yukon Territory compared to maxillae of Recent lynx and mountain lion (*Felis concolor*) from Canada.

Specimens	Sex	Measurements (mm)*				
		1	2	3	4	5
<i>Felis (Lynx) canadensis</i> .Pleistocene, Y.T.						
NMC 24966 Old Crow Loc. 11A	-	9.0	18.6	8.2	11.8	10.2
<i>Felis (Lynx) canadensis</i> .Recent, Canada						
NMC 34161 Y.T.	♂	9.0	17.3	8.1	11.3	9.0
NMC 34165 Y.T.	♀	7.7	16.6	7.5	10.9	8.8
NMC 34198 Y.T.	♂	9.8	16.5	8.0	11.0	8.6
NMC 34163 Y.T.	♂	9.2	16.4	7.3	11.0	8.9
NMC 32172 -	♂	9.4	15.9	7.7	10.5	8.9
NMC 34164 Y.T.	♂	8.5	15.2	7.7	10.6	8.2
<i>Felis concolor</i> .Recent, B.C.						
NMC 14344	♂	18.7	24.3	12.4	16.0	13.6
NMC 11269	-	24.5	24.1	13.0	15.6	12.1
NMC 29264	♂	20.7	23.0	12.3	15.2	12.9
NMC 11507	♀	-18.9	22.4	11.8	15.1	11.4
NMC 29263	♂	21.7	21.9	10.3	14.0	12.0
NMC 11508	♀	22.1	22.1	11.8	13.9	10.8

* 1 - Depth from maxillary - malar suture to alveolar margin of P⁴ above the paracone.

2 - P⁴ length.

3 - P⁴ width across protocone.

4 - Length from posterior margin of P⁴ metacone to the anterior margin of P⁴.

5 - Height of P⁴ metacone.

Table 49. Measurements of a Pleistocene lynx (*Felis (Lynx) canadensis*) mandible from the Yukon Territory compared to mandibles of Recent lynx from Canada.

Specimens	Sex	Measurements (mm) *	
		1	2
<i>Felis (Lynx) canadensis</i> .Pleistocene, Y.T.			
NMC 20322 Old Crow Loc. 29		17.5	8.2
<i>Felis (Lynx) canadensis</i> .Recent, Canada			
NMC 32172 -	♂	18.1	8.1
NMC 34198 Y.T.	♂	16.3	7.4
NMC 34161 Y.T.	♂	16.1	7.5
NMC 34164 Y.T.	♂	15.1	7.1
NMC 34165 Y.T. (young)	♀	12.8	6.9

* 1 - Depth of mandible below posterior root of M_1 .

2 - Thickness of mandible below posterior root of M_1 .

NMC 20322 from Old Crow Locality 29 is a right mandibular fragment containing a posterior part of the metaconid of RM_1 . It matches Recent specimens of the lynx in size and in all characters that are preserved. Notable similarities are the very gradual upward sweep of the anterior margin of the ascending ramus, the deep masseteric fossa extending anteriorly to a point below the posterior root of M_1 , the extremely flat medial surface of the mandible, and the size and position of the mandibular foramen. Among Recent Canadian specimens to which it was compared, the fossil is closest to a male, NMC 32172. The ramus is stained brown and shows signs of surface oxidation. The tooth fragment is darker.

Discussion

The Yukon fossils are considered to be of pre-late Wisconsin age. Geist (1953, p. 172) has briefly mentioned ("Lynx-rare") remains of this species from Pleistocene sediments near Fairbanks, Alaska, but they have not been described. The only Canadian record, apart from the Yukon fossils, is from Sangamon interglacial deposits at Medicine Hat, Alberta (Stalker and Churcher 1970). Remains of Wisconsin age have also been found in Idaho, Wyoming and Utah. Lynx fossils are rarely found in North America.

The origins and dispersal history of the lynx are difficult to understand without more and better evidence. At present, it seems most likely that the ancestor of the Canada and Eurasian lynx is the Issoire lynx (*Felis (Lynx) issiodorensis*) of the Villafranchian of Europe and possibly China. Evidently it had reached southern North America by early Pleistocene (late Blancan) time across the Bering Isthmus, for "*Felis* aff. *F. (Lynx) issiodorensis*" is reported in the Cita Canyon fauna of Texas by Hibbard (Skinner *et al.* 1972, p. 128). Compared to modern lynx it has a long face and body, and short legs. Perhaps the typical hunting methods and body of the northern lynx began to evolve in the middle Pleistocene when hares (*Lepus*) first entered Europe (Kurtén 1968, pp. 81-82). As the earliest certain finds of the Eurasian and Canada lynx are of Eem (Sangamon) interglacial age, I speculate that lynx arose in the coniferous forests of western Beringia during the middle Pleistocene, whence they dispersed westward to Europe and eastward across the Bering Isthmus during the Illinoian glaciation. The problem is complicated by the fact that large lynx-like felid remains are known from the Borchers fauna (Aftonian interglacial) of Kansas, and the Mullen II fauna (early Illinoian glacial) of Nebraska (Kurtén, personal communication 1976). It is conceivable that modern lynx stemmed from them, but too

little is known about these forms.

Felis (Lynx) canadensis is found only in northern North America, particularly in the broad boreal forest belt extending across Canada from the Yukon Territory to Newfoundland. It is common throughout the Yukon. It may occur well north and south of its normal range when hare populations are lowest in the boreal forest. The Canada lynx is a medium-sized cat with a short body, long legs with broad padded feet, a stubby tail and a thick coat. These cats prefer to live in dense boreal forest with thick undergrowth and windfalls, and their fossils are probably indicative of that type of paleoenvironment. They are generally solitary and nocturnal. For shelter they construct rough beds under rocky ledges or windfalls. Sometimes they use caves. Their populations fluctuate greatly, depending upon the abundance of hares, with peaks about 10 years apart. About three-quarters of their diet is made up of snowshoe hares (*Lepus americanus*), which evidently were fairly common in the Old Crow Basin during the late Pleistocene. Birds, such as ducks and ptarmigan, and voles make up most of the rest of their diet. Besides people, lynx have few predators except for mountain lions and wolves. In the forest they can escape wolves by climbing trees.

Felis (Puma) cf. concolor (mountain lion)

A single specimen of what appears to be a large mountain lion or cougar (Figure 47A-B, Table 50) has been collected from Yukon Pleistocene deposits. At the present time, mountain lions are occasionally seen within the southern border of the Yukon Territory (Youngman 1975, p. 153).

Referred specimen

NMC 24958 from Old Crow Locality 11A is an RP_4 lacking the roots. The complete crown seems to have been broken off leaving the roots in the mandible. All cusps are well worn, which in conjunction with the relatively large size of the tooth, suggests that an adult is represented. There is no evidence that the tooth differs in any characteristics from P_4 s of living mountain lions, but it averages about 30% larger in all measurements than Recent specimens with which it was compared. The height of the principal cusp is particularly great (approximately 40% larger) in relation to those of Recent mountain lions examined. NMC 24958 is much smaller than P_4 s of the American lion (*Panthera leo atrox*), but no dP_4 s were available for comparison. The morphological features of the specimen indicate its affinities with the mountain lion; the size difference seems worth noting



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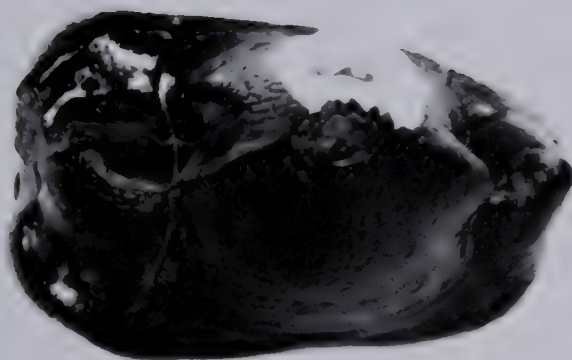


Figure 47. Crown of an RP_4 (NMC 24958, Old Crow
Locality 11A) tentatively referred to a
Pleistocene mountain lion (*Felis (Puma) cf.*
concolor). A. Lateral view.
B. Occlusal view.



A

3 CM



B

3 CM

Table 50. Measurements of a Pleistocene mountain lion (*Felis (Puma) cf. concolor*) P₄ from the Yukon Territory compared to P₄s of recent mountain lions from British Columbia.

Specimens	Sex	Measurements (mm)*			
		1	2	3	4
<i>Felis (Puma) cf. concolor</i> .Pleistocene, Y.T.					
NMC 24958 Old Crow Loc. 11A	-	19.1	11.5	10.9	13.4
<i>Felis (Puma) concolor</i> .Recent, B.C.					
NMC 11269	-	17.5	8.9	10.8	8.2
NMC 14344	♂	16.7	8.5	11.9	8.3
NMC 11508	♀	16.1	7.4	9.7	7.3
NMC 29264	♂	16.0	8.3	11.9	8.4
NMC 11507	♀	15.6	7.8	9.8	7.6
NMC 29263	♂	14.4	7.5	10.7	7.8

* 1 - P₄ length.

2 - P₄ width.

3 - Basal length of principal cusp of P₄.

4 - Height of principle cusp of P₄.

however, and the fossil may represent another species within the same subgenus (*Puma*), such as the giant mountain lion (*Felis (Puma) inexpectata*). Therefore, pending the recovery of more complete fossils, NMC 24958 is tentatively referred to *Felis (Puma) cf. concolor*. The specimen is stained black.

The Yukon fossil is almost certainly pre- late Wisconsin in age. This species has not been recorded previously from Pleistocene deposits of Canada or Alaska.

The mountain lion appears to be related to the larger, rangier giant mountain lion *Felis inexpectata*, which is known from the early Pleistocene (late Blancan) faunas of Cita Canyon and Blanco, Texas, and Curtis Ranch, Arizona, through the middle Pleistocene (Kansan) faunas of Mullen II, Nebraska, Cumberland Cave, Maryland and Conard Fissure, Arkansas. *Felis concolor* is fairly common in the late Pleistocene. It first appears in the late Illinoian fauna of Santa Fe River IIA (Webb 1974, Figure 2.2, Table 2.1) in Florida, continues through the Sangamon interglacial (Reddick IA, Florida; Cragin Quarry, Kansas), and has been reported from many sites of Wisconsin age from California to Florida and Idaho to Maryland (B. Kurtén, personal communication 1976). Presumably the species evolved

during the Illinoian glaciation. Evidently late Pleistocene mountain lions were larger on the average than those found in the same areas today (Merriam and Stock 1932, p. 207; Anderson 1968, p. 46), and it is worth noting that mountain lions are larger in size toward the northern limits of their range at the present time (Kurtén 1973, p. 4), which may help to explain the unusually large size of the Old Crow specimen.

The mountain lion, which is confined to America, has one of the most extensive distributions of any mammal in the Western Hemisphere. It originally occurred from Pacific to Atlantic (and this was apparently true during the late Pleistocene) and from the southern border area of the Yukon Territory to Patagonia in South America. Mountain lions are fairly large cats, which are known to have reached 8 feet (2.4 m) in total length and approximately 270 pounds (120 kg) in weight. They have long tails, and their well developed hind legs aid them in pouncing on prey. They occupy a wide variety of habitats so their fossils are not particularly useful as paleoenvironmental indicators. It seems to me, however, that they are not well adapted to surviving prolonged cold in relatively open areas - a thought suggested by their long tails, short coats and present

range south of the tundra. Therefore, it seems plausible that the fossil NMC 24958 would date to an interglacial rather than a glacial time in the Pleistocene of the Yukon. Cougars, like lynx, are generally solitary and nocturnal animals with keen senses. They are excellent climbers. Their lairs are usually caves or rock crevices, but they may shelter beneath overhanging banks or trees. Mountain lions stalk and feed primarily on large mammals, particularly white-tailed or mule deer. They also eat wapiti, moose, mountain sheep, porcupines, and many other species. Under extreme circumstances they will kill humans. Except for people, who often shoot them to protect livestock, mountain lions have few predators.

Panthera leo atrox (American lion)

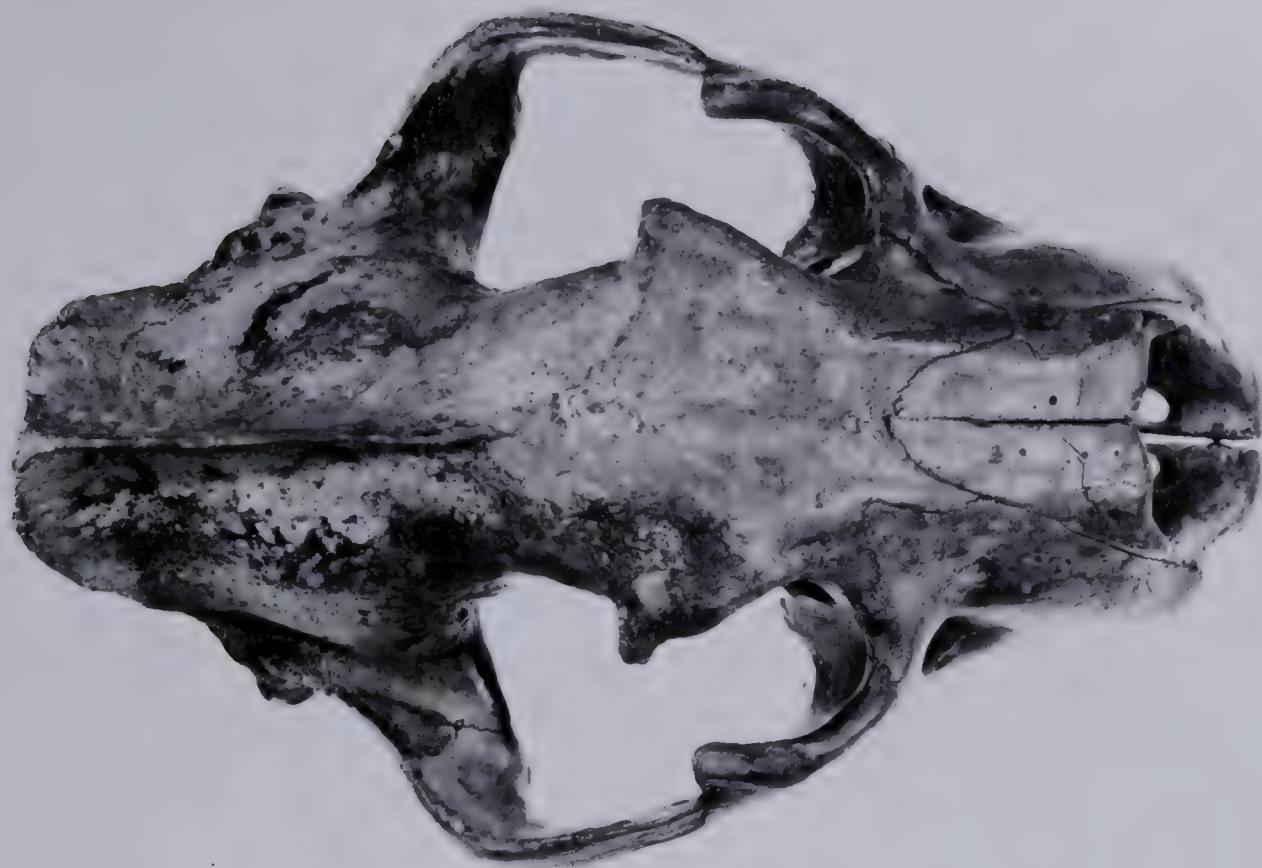
Remains of the American lion (Figures 48A-B, 49A-C, 50, Tables 51-54) are occasionally found in the Pleistocene deposits of the Yukon Territory. They are readily identifiable by their large size, and it is easy to see characters in most bones of the skeleton that differ from those of the scimitar cat (*Homotherium*) and the sabertooth cat (*Smilodon*) (Merriam and Stock 1932). The first American lion remains from Canada and the Yukon Territory were recorded in 1969 (Harington 1969). Since



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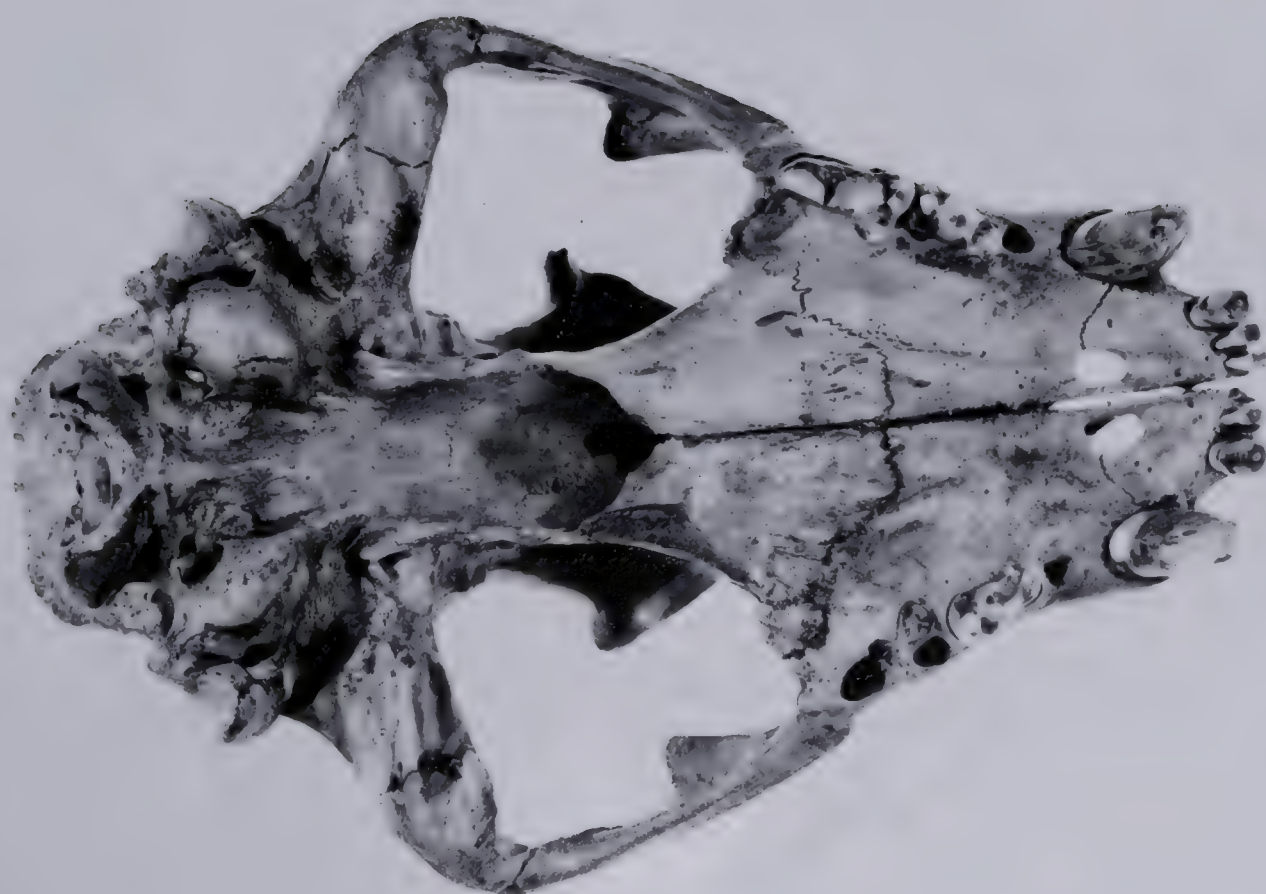


Figure 48. Cranium (NMC 13742, Dawson Locality 10)
of a Pleistocene American lion (*Panthera
leo atrox*).
A. Dorsal view. B. Ventral view.



5 CM

A



5 CM

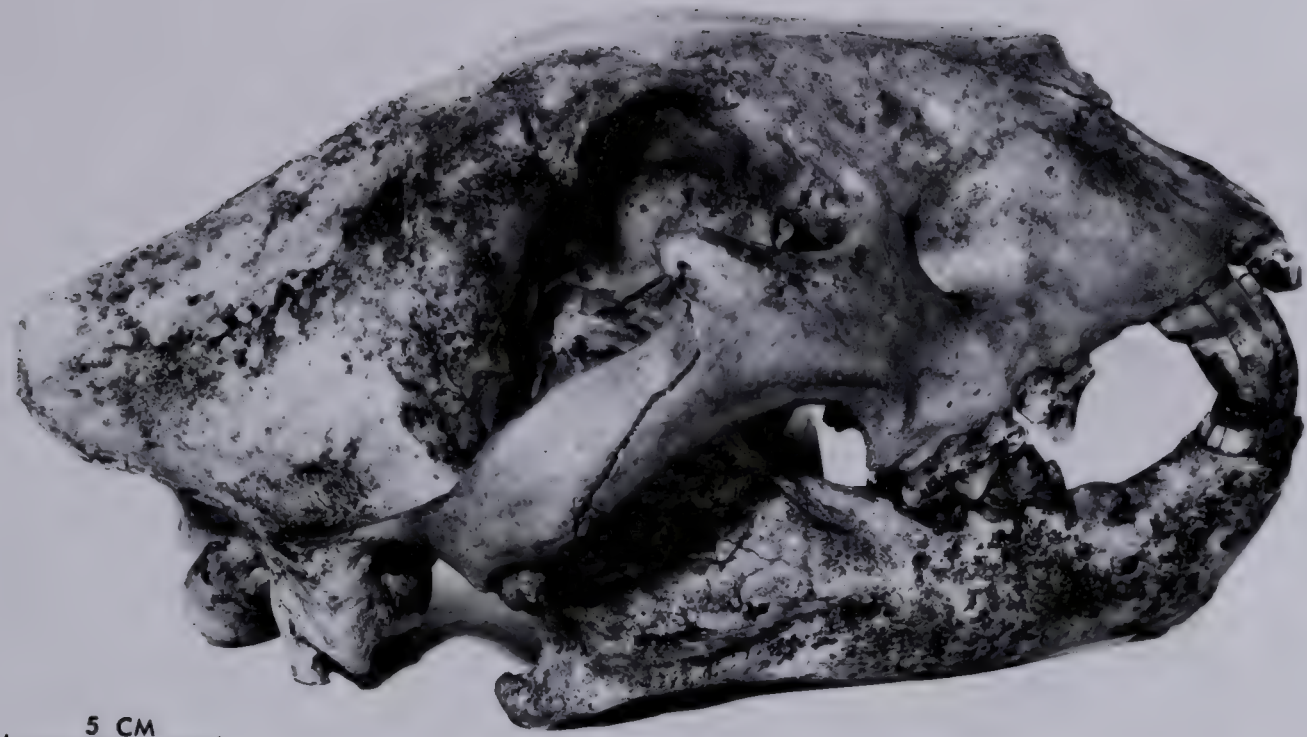
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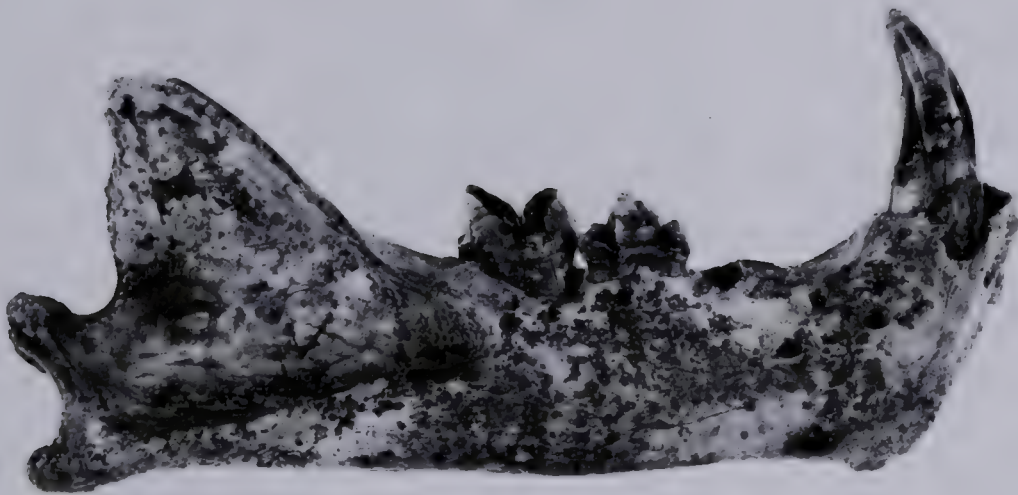
Figure 49. A. Right lateral view of cranium and articulated right mandible (NMC 13472, Dawson Locality 10) of a Pleistocene American lion (*Panthera leo atrox*).

B. Right lateral view of right mandible with RC_1 , and RP_4-RM_1 (NMC 13472, Dawson Locality 10).

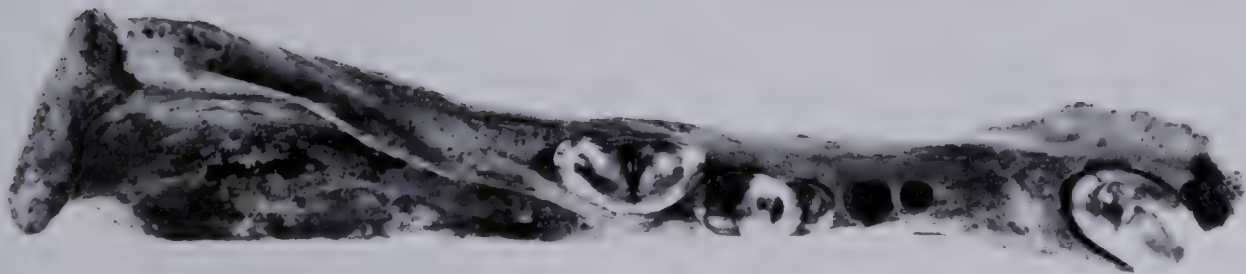
C. Occlusal view of right mandible NMC 13472.



A



B



C



Figure 50. Restoration of an American lion (*Panthera leo atrox*) attacking a Yukon wild ass (*Equus (Asinus) lambei*). Ink sketch by Bonnie Dalzell.



Table 51. Measurements of Pleistocene American Lion (*Panthera leo atrox*) crania from the Yukon Territory compared to those of Pleistocene American Lions from Rancho La Brea, California.

Specimens	Measurements (mm)*																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Panthera leo atrox</i> , Pleistocene, Y.T.																	
AMC 13742 Dawson Loc. 10	293.8	278.2	319.0	148.6	83.8	70.4	53.0	94.8	70.3	107.8	66.4	214.3	87.0	132.5	29.6	130.3	63.7
NMC 12230 Dawson Loc. 7	-	-	-	-	101.1	-	-	-	77.2	114.9	72.4	253.4a	-	-	28.8	144.2a	71.4
NMC 29013 Dawson Loc. 16	-	-	-	-	93.3	-	-	-	-	-	67.2	-	-	-	27.2	146.1	65.2
<i>Panthera leo atrox</i> , Pleistocene, Rancho la Brea, Calif. (Gericium and Stock 1932, p. 173)																	
M	353.1	331.6	396.2	176.4	94.7	97.1	62.3	115.9	84.9	114.2	78.8	250.4	89.5	126.8	26.9	146.5	69.6
OR	290- 424.3	269- 404.7	310.3- 467.5	142.9- 212	80- 112.5	79.2- 114	47a- 73	98- 141.4	68.8- 106.6	99- 132	71- 89	203a- 304.3	76- 108.4	110- 147.8	21.1- 35.9	122.8- 173.6	58.4- 78.6
N	17	18	16	16	16	13	16	18	15	14	17	15	16	17	18	14	17

* 1 - Condylobasal length.

2 - Basal length.

3 - Total length.

4 - Palatal length.

5 - Posterior of glenoid cavity to posterior of condyles.

6 - Nasal length.

7 - Width of nasal opening.

8 - Rostral width at canines.

9 - Least width between orbits.

10 - Width across postorbital processes.

11 - Width at postorbital constriction.

12 - Zygomatic width.

13 - Posterior palatal width between inner roots of upper carnassials.

14 - Width across posterior alveoli of upper carnassials.

15 - Width across bulla.

16 - Mastoid width.

17 - Width across condyles.

Table 53. Measurements of Pleistocene American lion (*Panthera leo atrox*) mandibles and lower dentitions from the Yukon Territory compared to those of Pleistocene American lions from Rancho La Brea, California.

	Measurements (mm)*																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Panthera leo atrox</i> .																				
Pleistocene, Y.T.																				
NMC 13742 Dawson Loc. 10	218.6	70.8	42.2	47.5	20.2	95.0*	42.4	-	15.9	20.4	14.6	-	-	25.0	12.0	12.3	27.5	13.5	116.7	70.0
NMC 29014 Dawson Loc. 16	248.0	79.7	42.4	50.3	22.3	123.2*	54.1	58.3	22.1	26.2a	17.2	-	-	25.9	11.8*	12.4	-	-	126.3	71.7
NMC 29187 Sixtymile Loc. 3	259.9	81.2	50.2	55.8	24.9	126.6	50.5	61.7	22.5	29.3*	21.4	18.7	10.6	-	-	-	28.9	14.8	133.5	79.1
NMC 15433 Old Crow Loc. 14N	-	-	-	-	-	-	-	-	-	27.9	18.8*	-	-	-	-	-	-	-	-	-
<i>Panthera leo atrox</i> .																				
Pleistocene,																				
Rancho La Brea, Calif.																				
(Merriam and Stock 1932,																				
pp. 176-177)																				
M	241.0	78.4	50.3	54.1	24.9	121.7	51.6	60.1	22.4	26.8	20.0	19.5	11.1	29.1	14.3	13.3	29.7	14.9	137.2	78.2
OR	206-	67.2-	38.9-	46.0-	20.0-	96.3-	42.0-	44.5a-	18.4-	21.8-	15.1-	17.0-	8.9-	25.8-	12.0-	11.9-	26.9-	13.0-	116.4-	68.3-
	318	99.3	60.7	67.1	36.9	150.0	66.4	74.9	27.2	30.4	22.0a	21.6	13.2	32.3	16.9	15.0	33.9	17.5	156.7	89.0
N	16	16	16	16	16	15	16	16	16	11	11	15	15	16	16	16	16	16	14	16

* 1 - Length from symphysis to condyle.

2 - Length of anterior border of symphysis.

3 - Mandibular depth at anterior end of P₄.

4 - Mandibular depth below posterior end of M₁.

5 - Thickness of mandible below posterior end of M₁.

6 - Height of ascending ramus (angle to coronoid process).

7 - Height from angle to condyle.

8 - Width of condyle.

9 - Maximum depth of condyle.

10 - C₁ length.

11 - C₁ width.

12 - P₃ length.

13 - P₃ width.

14 - P₄ length.

15 - P₄ width.

16 - P₄ length of principal cusp.

17 - M₁ length.

18 - M₁ width.

19 - Alveolar length C₁-M₁.

20 - Alveolar length P₃-M₁.

Table 54. Measurements of Pleistocene American lion (*Panthera leo atrox*) forelimb bones from the Yukon Territory compared to those of Pleistocene American lions from Rancho la Brea, California.

Specimens	Measurements (mm)*							
	Humerus				Ulna			
	1	2	3	4	5	6	7	8
<i>Panthera leo atrox</i> .Pleistocene, Y.T.								
NMC 11706 (humerus) Dawson Loc. 28 { same	32.5	54.6	90.6	29.1	-	-	-	-
NMC 11707 (ulna) Dawson Loc. 28 { individual	-	-	-	-	47.0	62.9	42.5	17.9
NMC 27478 (humerus) Old Crow Loc. 62	34.8	41.8	88.8	29.2	-	-	-	-
NMC 25191 (ulna) Dawson Loc. 16	-	-	-	-	48.4	-	38.8	21.2
NMC 16801 (ulna) Old Crow Loc. 14N	-	-	-	-	51.7	-	39.6	25.3
<i>Panthera leo atrox</i> .Pleistocene, Rancho la Brea, Calif. (Merriam and Stock 1932, Tables 42, 44)								
M	36.8	60.3	100.1	32.8	61.4	78.8	50.9	22.9
OR	33.0-	53.4-	85.7-	29.5-	48.0-	68.5-	42.5-	20.7-
	41.4	70.0	111.3	36.0	69.7	87.8	57.7	25.0
N	9	9	9	9	7	7	7	7

*1 - Midshaft width.

2 - Midshaft depth.

3 - Distal width.

4 - Minimum anteroposterior diameter of articulating surface for ulna.

5 - Greatest width of greater sigmoid cavity.

6 - Depth from posterior border to top of coronoid process.

7 - Shaft depth at proximal end of tendon scar.

8 - Shaft width at proximal end of tendon scar.

then, several specimens have been collected from the Dawson, Sixtymile and Old Crow areas. Some of the more complete fossils are described.

A few preliminary remarks seem necessary before describing the specimens. There has been a dispute over the affinities of the American lion. Leidy (1853, p. 320), in his description of the type specimen "*Felis atrox*" (the anterior half of a mandible from Mississippi), mentioned several points in which he considered it was closer to a lion than a tiger. Merriam and Stock (1932) gave the first detailed description of the species, basing it on an abundant sample of good specimens from the Rancho La Brea tar pits in California. Primitive features of the species, such as relatively small brain size, and structural similarities to both the lion and tiger, suggested to them that it approached the ancestral group from which the large cats may have been derived. It is surprising that Merriam and Stock (1932, pp. 190-195) did not refer this large American cat to the Eurasian cave lion, considering the results of their comparisons. They (Merriam and Stock 1932, pp. 186-187) apparently refrained from this because of a lack of knowledge then concerning Pleistocene faunal relationships of North America and Eurasia. Evidently they knew of no cave lion remains closer to North America than

the Urals. Because of this, and a report of "tiger" remains from northern Siberia, they thought a closer relationship between the Rancho La Brea animals and the tiger, rather than the lion, might be implied from the zoogeographical data alone. Also, they apparently expected that an ancestral form might be found in the North American Tertiary. Simpson (1941) remarked that "*Panthera atrox*" is not a lion and might be called a giant jaguar (a term first used by Freudenberg in 1910), specifically distinct from the South American jaguar *Panthera onca*, but nevertheless related to it. This opinion held sway among American paleontologists until recently, when more detailed morphological and zoogeographical studies have clearly demonstrated that this large American cat is a lion, closely allied to, if not consubspecific with the Eurasian cave lion (Harington 1969, pp. 1282-1286; Vereshchagin 1971; Hemmer 1974).

Referred specimens

NMC 13742 from Dawson Locality 10 is a rather small, complete cranium with all teeth except LI^1 , both P^2 s, LP^3 (the anterointernal root is still in its socket) and both M^1 s. The palatine and lacrimal bones below the orbits are damaged. A right mandible associated with the cranium lacks only the incisors, RP_3 and bone on the

superior and posterior margins of the coronoid process. The teeth of this skull are well worn, particularly the upper incisors and the shearing surfaces of the carnassials, which, combined with complete fusion of the frontal suture, the basioccipital - basisphenoid suture, and the strong development of the sagittal crest, indicate that an adult is represented. The palatal bones are misleading with regard to age determination, for obviously they have sprung apart after the animal's death, probably as a result of drying after the specimen was released from the permafrost. The relatively slender canines, and smallness of the cranium and mandible may be indicative of a female (Stock 1965, pp. 39-40). The specimen is tan with a dark gray surface mottling (manganese?). These fossils came from near the interface of a gold-bearing gravel somewhat more than 5 inches (13 cm) thick and an overlying 25 to 50-foot (7.6 to 15.2 m)-thick unit of organic silt or muck. Evidently the lion represented by NMC 13742 died near the locality where it was found.

NMC 12230 from Dawson Locality 7 is a cranial fragment posterior to the nasals. Zygomatic arches are lacking except for most of the right zygomatic process of the temporal. Mastoid and paroccipital processes are heavily worn or missing, and the supraoccipital is broken

off. The specimen is of average size for the American lion. Fusion of the basioccipital - basisphenoid suture (see Miller 1968, p. 5), and the marked development of the sagittal crest suggest that the specimen represents an adult male. Signs of surface erosion show that the specimen was transported for a short distance. The fossil was collected near the interface of the gravel and muck at Quartz Creek. It has been described previously (Harington 1969, p. 1277).

Another posterior cranial fragment, NMC 29013, was collected from Dawson Locality 16. It is similar to NMC 12230 except that bone anterior to the postorbital processes is missing. Only the stub of the temporal process of the left zygomatic arch is preserved. The sagittal crest is well developed.

NMC 24234 from Old Crow Locality 22 is an LP⁴ slightly larger than that preserved in NMC 13742, and of approximately average size compared to a sample from Rancho La Brea. The vestigial cusp of the protocone is evident, as is an extensive facet on the lingual surface of the paracone and metacone. The cementum on the three roots of this tooth is stained rusty brown, while the enamel is ivory colored with a grayish

mottling, as seen in teeth from the Dawson Area. It may be of late Wisconsin age.

NMC 29014 from Dawson Locality 16 is a right mandible lacking the incisors, the tip of the canine and RM_1 . The tips of the coronoid and angular processes are lacking. Part of a groove-like wear facet made by RC^1 is seen on the posterolateral surface of the lower canine. Wear is moderate on the principal and posterior cusps of RP_4 .

NMC 29187 from Sixtymile Locality 3 is a left mandible lacking the incisors, the tip of the canine (like NMC 29014 it also shows a groove-like facet made by the upper incisor), and most of the crown of LP_4 . The metaconid blade of LM_1 is heavily worn and its anterior portion appears to have been broken, then worn. It is the largest of the three mandibles described, but is only of average size relative to American lion mandibles sampled from the tar pits of Rancho La Brea. Pitting around the alveolar margins, the high degree of wear on the teeth and the massive canine suggest that an old male is represented. A slight peculiarity of the specimen is that there are two posterior mental foramina instead of the single foramen usually found beneath the anterior

root of P_3 . The specimen is pale buff in color.

NMC 15433 from Old Crow Locality 14N is an LC_1 with a broken root tip and a 20 mm long x 5 mm wide groove-like wear facet on the posterolateral surface. It is stained blackish brown and has approximately eight ridge-like bands girdling the cementum of the root, which may be annuli. The characteristic ridge running from the cingulum to the tip of the enamel on the anteromedial surface is present. The tooth is blackish brown and may be of pre- late Wisconsin age. Generally, the teeth of American lions from the Yukon Territory are smaller than those from farther south (Rancho La Brea).

NMC 11706 from Dawson Locality 28 is a right humerus lacking the proximal end. It is smaller than an American lion humerus (UCMP 2051) from Rancho La Brea with which I compared it, but has the same morphological features. It was found with and articulates with the ulna NMC 11707.

NMC 11707 from the same locality is a right ulna, lacking the distal end, which articulates with NMC 11706. The surfaces of both bones are bright orange brown, and are covered with clearly defined rootlet

impressions, not inconsistent with decay in a grassy loess-steppe environment. These specimens have been described in greater detail and illustrated (Harington 1969, p. 1280, Plate III).

NMC 27478 from Old Crow Locality 62 is the distal half of a left humerus that compares closely in size and in all morphological features with NMC 11706.

NMC 25191 from Dawson Locality 16 is a right ulna lacking the extremities. It is stained brown. NMC 16801 from Old Crow Locality 14N is the proximal part of a right ulna lacking the olecranon region. It is stained dark brown and may be of pre- late Wisconsin age.

A right metatarsal IV (LUM 1. 176) from Dawson Locality 32 has been described by Harington and Clulow (1973, p. 700). Probably it is of late Wisconsin age.

Discussion

Evidently American lions were widespread in the Yukon part of the Eastern Beringian refugium. Most of the specimens from near Dawson and Sixtymile are probably of late Wisconsin age. Except for NMC 24234, the Old Crow fossils are deeply stained and are likely pre-late Wisconsin in age.

American lion fossils have been reported from many parts of Alaska such as the Fairbanks area (Guthrie 1968b), Lost Chicken Creek near the Yukon - Alaska border (Whitmore and Foster 1967), and the Kaolak River near the arctic coast (Harington 1969, pp. 1280-1282). Probably most of these specimens are of Wisconsin age. A specimen mentioned as "*Felis* sp. (large cat)" from the loess at Gold Hill near Fairbanks may represent the American lion. If so, it would probably be of Illinoian age (Péwé 1975a, p. 96).

The only Canadian records, apart from the Yukon fossils, are from near Bindloss (Harington 1971) and Medicine Hat in southern Alberta (Stalker and Churcher 1970). The Medicine Hat material is from deposits of Sangamon interglacial age.

In the United States, the earliest (probably Illinoian) record of *P. leo atrox* is from American Falls, Idaho. Specimens of Sangamon interglacial age, or early Wisconsin to Sangamon age, are known from Cragin Quarry, Kansas and Easley Ranch, Texas, respectively. Fossils of this species have been collected at many localities of Wisconsin age in the United States, and from Tequixquiac, Mexico (Freudenberg 1910) and the Talara

tar-seeps, Peru (Lemon and Churcher 1961).

Probably central Asia was the dispersal centre of the genus *Panthera* (Thenius 1967, p. 138). The earliest known large cat having both lion and tiger-like characters is *Panthera* sp. from the Villafranchian (Bed II) deposits at Olduvai Gorge, East Africa (Ewer 1965, p. 21). This cat seems to have been very closely related to *Panthera leo fossilis* of the early middle Pleistocene of Europe (Mauer, Mosbach, Scharzfeld and Obrigheim), which probably gave rise to the cave lion *Panthera leo spelaea* and, I think, the American lion *Panthera leo atrox*, which are characterized by more efficient crushing teeth (Schütt 1970, pp. 213-214). The cave lion first occurred in Europe during the middle to late Pleistocene (Schütt 1970) and evidently lived there continuously until the last glaciation (Kurtén 1968, pp. 85-87). "*Panthera youngi*", with affinities to both the cave lion and American lion, appeared in northeastern China (Choukoutien Locality 1) during the late middle Pleistocene. I suspect that this cat is very close to the transition between *P. leo fossilis* and the "*spelaea* group" (the northern Holarctic lions including *P. leo spelaea* in Europe and Siberia and *P. leo atrox* in America; the other group being the

"leo group" of the southern Palearctic, Ethiopian and western Oriental regions (scheme slightly modified from that of Hemmer 1974, p. 271)).

Panthera leo atrox ranged from northern Alaska to northwestern Peru, and from California to Florida (Harington 1969, Figure 1; Harington 1971, Figure 1). It has a temporal range extending probably from the Illinoian glacial, and certainly from the Sangamon interglacial, to the end of the Wisconsin glacial. The only direct radiocarbon date of the American lion from Beringia is on tendon from a tibia from Alaska, which yielded a date of $22,680 \pm 300$ years B.P. (SI-456), indicating the species was there near the peak of the late Wisconsin glaciation. Many of the Yukon specimens appear to be of similar age. The most recent remains seem to be from Jaguar Cave, Idaho, where hearths containing its bones have been radiocarbon dated at $10,370 \pm 350$ years B.P. (Kurtén and Anderson 1972, p. 22).

In summary, the cave lion *P. leo spelaea* was common in eastern Siberia during the late Pleistocene (from the Illinoian glaciation to the close of the Wisconsin glaciation). Its remains have been reported from the Yensei River in the west of that region to the

Alazeya River in the east (Vangengeim 1961, p. 141) – about 1,000 miles (1,600 km) west of the nearest known specimen of *P. leo atrox* from the Kaolak River in northern Alaska. That distance is perhaps of little significance considering the wide-ranging habits of the cave lion, its adaptability to cool climatic conditions, and the breadth of the land connection between Siberia and Alaska during the late Pleistocene glaciations. The presence of bison, horse and mammoth herds on the grassy Bering Isthmus probably made it very attractive to lions. Therefore, the ancestral stock (*P. leo spelaea*) that gave rise to *P. leo atrox* probably crossed the Bering Isthmus from Siberia to North America during the Illinoian glaciation. Lions had penetrated the North American Plains by late Illinoian or early Sangamon time. As the Wisconsin ice spread, American lions were isolated in refugia to the north (Eastern Beringia) and south. Toward the end of the Wisconsin glaciation they ranged the southwestern half of the United States, penetrating as far south as Mexico and Peru. Some barrier, probably rather dense forests, seems to have prevented their movement into the northeastern United States and eastern Canada. The large lions of northern Eurasia and America became extinct at the close of the Wisconsin glaciation, probably following the decline of their large prey.

American and cave lions seem to have been larger than most living lions. Intriguing evidence indicates that these "*spelaea* group" lions had a faintly striped coat. A rather detailed wall engraving of a cave lion by a Paleolithic artist at Combarelles, France (Koby 1941, Figure 8) suggests that it had pale stripes and a slight mane. Probably it had a thick coat too - perhaps like the Amur tiger - as an adaptation to cold northern climates (Cornwall 1968, p. 1311). Gromov (1935, pp. 166-167) has described a small mammoth tusk figurine of a man wearing the whole skin of an animal with a long tail and head covering the wearer's head from the upper Paleolithic site at Mal'ta in the Soviet Union. The surface of the skin is striped, and Gromov suggests that the only animal pelt that could be depicted is that of a cave lion.

Probably the "*spelaea* group" lions were much like the modern lion in preferring open grassland and parklands. Their fossils are generally found with remains of other Pleistocene mammals (e.g. on the New Siberian Islands; at Lost Chicken Creek, Alaska; Gold Run Creek, Yukon Territory and Rancho La Brea, California) with those habitat preferences. They seem to have been well adapted to an arctic steppe environment. Probably heavy forests covering much of eastern North America during the late Pleistocene prevented

American lions from flourishing there.

Presumably American lions were gregarious and hunted in groups like African lions. They may have sheltered in caves, rock fissures or steep canyons, lining their dens with dried leaves or grass like Amur tigers (Stroganov 1969, p. 491) – large cats that have likewise adapted to cold climates. According to their anatomical structure, American lions were at least as fleet as African lions which are able to reach speeds of 30 miles (48.3 km) per hour in bursts when hunting (Boorer 1971, p. 91). Perhaps they were best adapted to feeding on the American bison (e.g. *Bison crassicornis* and *Bison latifrons*). Probably they also hunted wild asses and horses, such as *Equus (Asinus) lambei* and *Equus scotti*. Perhaps people were their only predators, although they undoubtedly had numerous competitors among the other large carnivores of the North American late Pleistocene, such as the short-faced bears, brown bears, wolves and wolverines. Remains of American lions among refuse in an archeological site at Jaguar Cave, Idaho, suggest that Paleo-Indians may have hunted or eaten them.

Homotherium serum (American scimitar cat)

Only three specimens from Pleistocene deposits of the Yukon Territory are referred to *Homotherium serum* (Figures 51A-C, 52A-C, Table 55). Evidently the scimitar cat was found in both Old Crow and Dawson areas, but was rarer in this part of Eastern Beringia than the American lion (*Panthera leo atrox*). The first specimen from Canada and Eastern Beringia was reported in 1970 (Harington 1970, p. 39). It extended the known range of the species over 2,000 miles (3,218 km) northward.

I have found no clear evidence that the saber-tooth cat, *Smilodon*, occupied the Yukon Territory during the Pleistocene. Its presence in Alaska has been mentioned by Geist (1953, p. 172), who merely states: "Saber tooth Tiger - uncommon", and later (Geist 1956, p. 201) "...only rare occurrences of camel and sabertooth cat are reported." Guthrie (1968b, p. 353) indicates that remains of *Smilodon* sp. were collected at Cripple Creek near Fairbanks, but in a colored wall chart accompanying a later publication, Guthrie (1972) illustrates and identifies *Homotherium serum* as the only "saber-toothed cat." Despite these reports, R. Tedford (personal communication 1976) informs me that he has not seen fossils of *Smilodon* in the extensive Frick

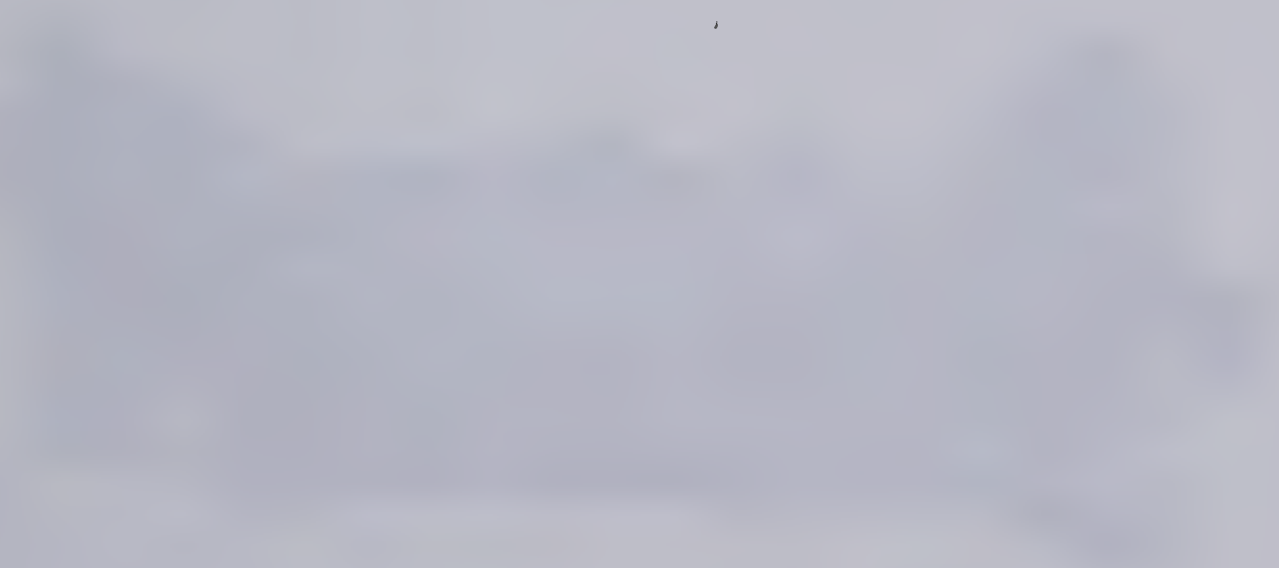


Figure 51. Right mandible with damaged RP_4 - RM_1
(NMC 12457, Old Crow Locality 21) of a
Pleistocene American scimitar cat
(*Homotherium serum*).

- A. Lateral view.
- B. Occlusal view.
- C. Medial view.

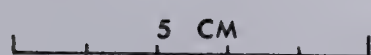
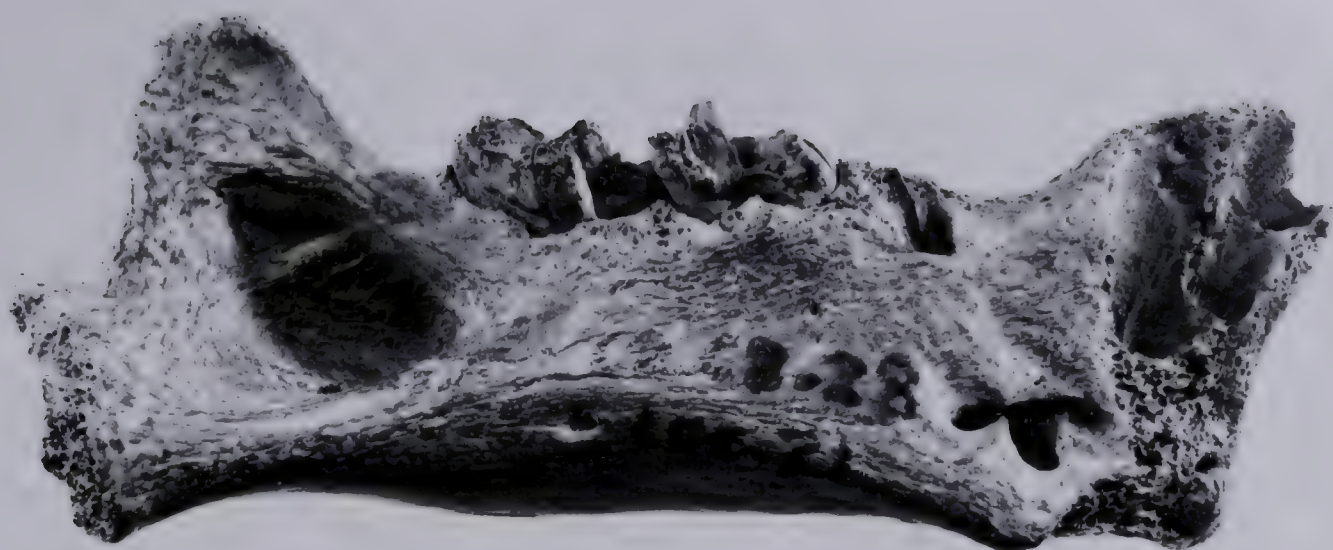
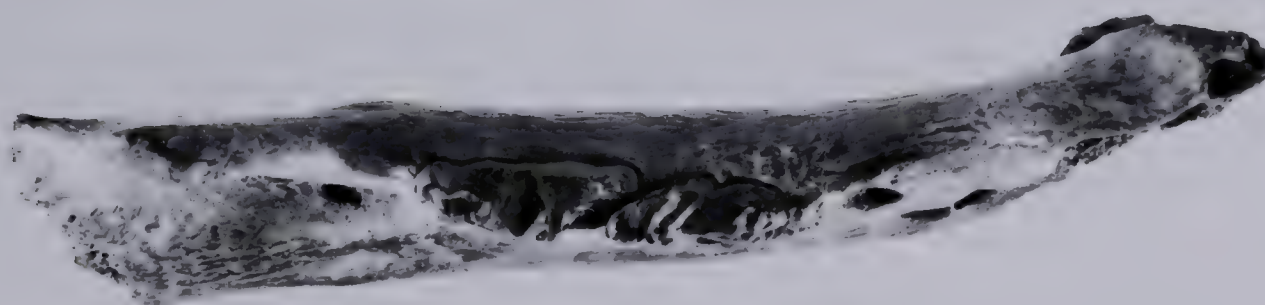
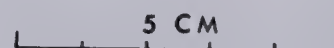
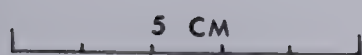
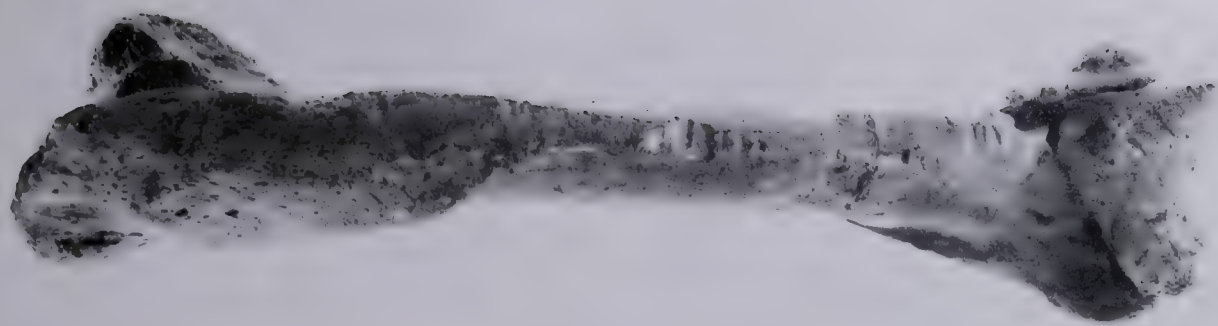
**A****B****C**

Figure 52. Distal end of a damaged right humerus (NMC 7758, Dawson Locality 9) of a Pleistocene American scimitar cat (*Homotherium serum*) (left) compared to a damaged right humerus of a Pleistocene American scimitar cat (TMM 933-2206, Friesenhahn Cave, Texas) (right).

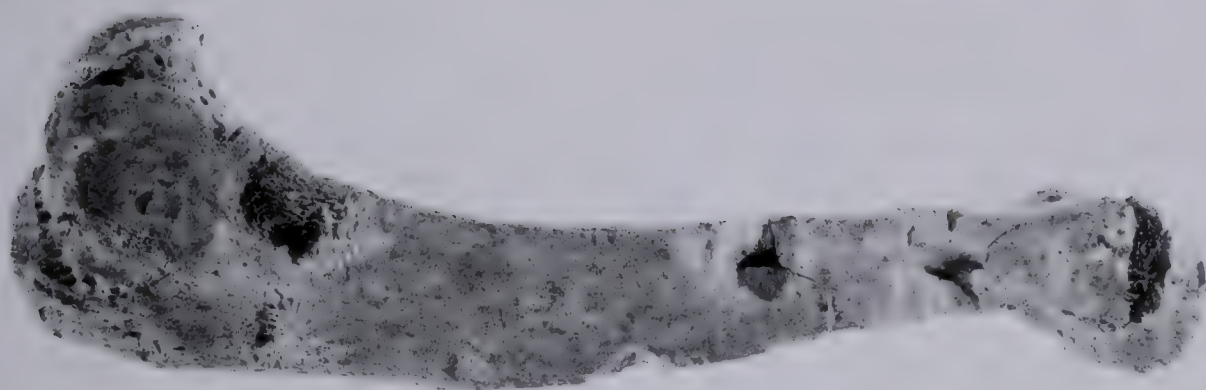
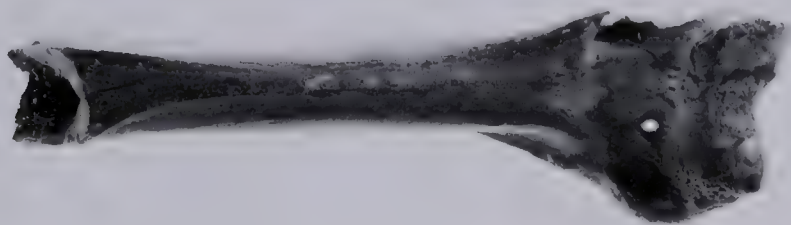
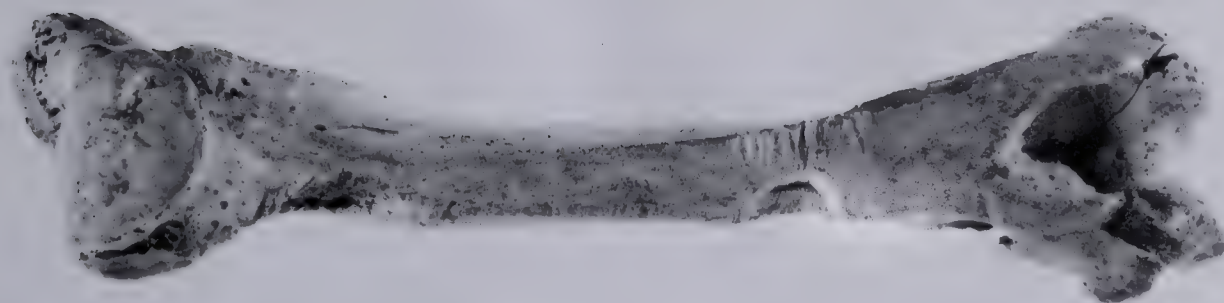
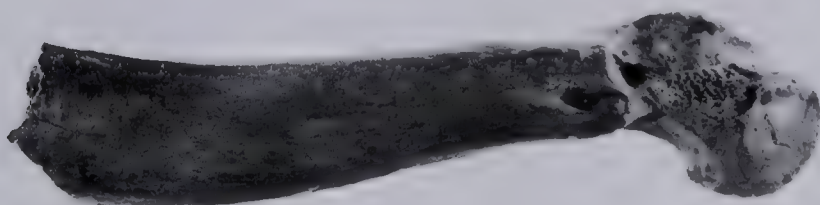
A. Anterior view.

B. Medial view.

C. Posterior view.



A

B
5 CM

C



Table 55. Measurements of a Pleistocene scimitar cat (*Homotherium serum*) mandible from the Yukon Territory compared to mandibles of American scimitar cats from the Pleistocene of Texas, *Homotherium latidens* from the Pleistocene of England, *Ischyrosmilus johnstoni* from the Pleistocene of Texas, and the sabretooth cat (*Smilodon* sp.) from the Pleistocene of California.

Specimens	Measurements (mm)*												
	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Homotherium serum</i> . Pleistocene, Y.T. NMC 12457 Old Crow Loc. 21	47.0	48.2	21.1a	50.2	79.2	65.9	53.2	32.7 [†]	45.0 [†]	24.0	9.0	31.8	10.9
<i>Homotherium serum</i> . Pleistocene, Texas Friesenhahn Cave (Neade 1961, Table 1)													
M	41.9	42.9	18.3	41.2	77.7	62.9	47.6	32.9	51.5	19.2	8.8	27.6	11.2
OR	38.0- 49.7	39.5- 47.5	17.7- 19.8	38.7- 45.0	71.0- 83.0	58.0- 67.0	47.2- 48.3	28.5- 43.6	43.0- 65.5	18.2- 20.4	8.1- 9.4	25.6- 30.6	10.1- 12.8
N (includes right and left mandibles of TMM-933-1)	5	7	8	6	6	5	6	4	5	9	9	10	10
<i>Homotherium latidens</i> (cont.). Pleistocene, England, Kessingland (B. Kurtén, personal communication 1969) Catalog number unknown	43.4	48.3	21.9**	43.5	79.3**	-	55.6**	-	45.0	21.5	8.2 [†]	31.8	11.3 [†]
<i>Ischyrosmilus johnstoni</i> . Pleistocene, Texas, Cita Canyon (Vawby 1965, Table 1)													
WT 1236	43.7	-	-	-	82.0	72.5	48.9	42.0a	-	22.3a	10.3	28.5a	13.7a
PCMP 66466	35.0 [†]	-	-	-	-	65.0	46.5	37.0	-	20.4	9.7	26.0 [†]	13.6 [†]
WT 2615	32.3	-	-	-	55.0	56.0	46.0	29.0	-	19.6	-	27.0	-
<i>Smilodon</i> sp. Pleistocene, Calif. Rancho La Brea (Merrill and Stock 1932, Table 5)													
M	33.9	40.3	21.4	33.8	68	78.2	-	-	-	29.1	14.3	29.7	14.9
OR	27.3- 40.4	36.0- 45.6	18.7- 25.0	30.7- 44.0	58.0- 76.3	68.3- 89.0	-	-	-	25.8- 32.3	12.0- 16.9	26.9- 33.9	12.4- 17.6
N	25	25	25	25	25	16	-	-	-	16	16	16	16

* 1 - Minimum mandibular depth at diastema.

2 - Mandibular depth below posterior end of M₁.

3 - Mandibular thickness below M₁.

4 - Depth, angle to summit of condyle.

5 - Depth, inferior border of angle to apex of coronoid process.

6 - Alveolar length P₃-M₁.

7 - Alveolar length P₂-M₁.

8 - Diastema length (C₁-P₃ alveoli).

9 - Alveolar length C₁-P₄.

10 - P₄ length.

11 - P₄ width.

12 - M₁ length.

13 - M₁ width.

** Measurements taken from a scaled photograph.

collection of Pleistocene mammal remains from Alaska housed in the American Museum of Natural History.

Presumably, the records of *Smilodon* from the Fairbanks area were actually based on *Homotherium* fossils. This does not mean that *Smilodon* will never be reported from Pleistocene deposits of Eastern Beringia.

Referred specimens

NMC 12457 from Old Crow Locality 21 is a right mandible with partly damaged RP_4 and RM_1 and partial sockets for RP_3 , the canine and incisors. Most of the blade of RP_4 is broken away. The anterior jaw flange and the angle and condyle of the mandible are lacking. The apex of the coronoid process appears to have been slightly eroded. The high degree of wear on RM_1 and the relatively large size of the mandible suggest that an old individual is represented. Morphological features of the specimen that characterize *Homotherium serum* are: (a) masseteric fossa more highly developed than in the sabertooth cat, *Smilodon*, or the American lion, *Panthera leo atrox*, and reaching maximum inflection at its anterior extremity; (b) coronoid process low and rounded as in *Smilodon*, not high and overhanging the condyle as in the American lion; (c) a flange was present on the anterolateral part of the mandible as in *Smilodon* and unlike the American lion; (d) the least depth of the

mandible below the diastema is greater than in *Smilodon*.
(e) length of the diastema between alveoli for C_1 and P_3 , and the C_1 - P_4 length, are clearly less than in *Smilodon*;
(f) P_4 and M_1 are narrower than those of *Smilodon* or *Panthera leo atrox*; (g) P_3 is present as in *Homotherium serum*: it is usually absent in *Smilodon*. The socket indicates that P_3 in the Yukon specimen had two fused roots as in *H. serum* (Churcher 1966, p. 269) and *Ischyrosmilus johnstoni* from earliest Pleistocene (late Blancan) deposits at Cita Canyon, Texas (Mawby 1965, p. 577); (h) a posterior mental foramen is well developed near the inferior margin of the mandible below M_1 as in *H. serum* (Meade 1961, Plate 1c): it is not apparent in *Smilodon* or the American lion as illustrated by Merriam and Stock (1932), and this part of the type mandible of *Ischyrosmilus johnstoni*, unfortunately, is missing (Mawby 1965, Figure 2). NMC 12457 is larger in most measurements than mandibles of *H. serum* from Friesenhahn Cave, Texas recorded by Meade (1961), but is very close in size and shape to *H. latidens* from England. It appears to be within the general range of measurements for *Ischyrosmilus johnstoni*, but more careful comparisons are required to understand the affinities of these two scimitar cats.

NMC 12457 differs from other scimitar cat mandibles I have seen in the confluence of the two anterior mental foramina. Usually these foramina are well separated. Perhaps this confluence has resulted from a shortening of the mandible anterior to P_3 . Pending further evidence, this feature is not considered to be of taxonomic significance; nor is the rather large size of the mandible compared to other *H. serum* specimens from Texas. Clines are detectable among other large cats such as the mountain lion, in which body size increases toward the northern limits of the species' range. In this case increased size could also be a function of the relatively old age of the individual. The mandible is stained dark brown, suggesting that it was permeated by mineral-bearing groundwater during a relatively warm period prior to formation of permafrost in the area during the late Wisconsin. I infer that the mandible is of late Pleistocene and probably pre- late Wisconsin age.

NMC 24216 from Old Crow Locality 66 is a fragment of an LC^1 or "scimitar" that was originally located between the tip and the uppermost exposed part of the canine. The specimen is only 49.7 mm long. Part of the slightly convex anterior margin of the canine fragment is serrated as in *Homotherium* and *Smilodon*.

The posterior margin and lower tip of the tooth are lacking. Its transverse diameter is 10.4 mm and its estimated anteroposterior length is about 28 mm. These proportions best fit the canines of *H. serum*, which are more compressed laterally and smaller than in *Smilodon*. The fossil is tentatively referred to *Homotherium serum*. It is stained black and appears to be of pre- late Wisconsin age.

NMC 7758 from Dawson Locality 9 consists of the distal two-thirds of a right humerus, lacking part of the lateral condyle and the proximal part of the medial epicondylar region. The anterior surface of the distal articulation is damaged, and deep subparallel gnaw marks are seen on the proximal end of the broken shaft on the lateral surface. They are opposed by shallower, subparallel marks having the same orientation on the medial surface. I think they were made by a medium to large carnivore, such as a fox, wolverine or wolf. The origin of the marks on the lower part of the shaft is less certain. There, shallower marks on the anterior surface are parallel to deeper slashes posterior to the entepicondylar foramen. It is an unusual coincidence that gnaw marks, evidently made by rodents in this case, appear on similar parts of a right humerus of

Homotherium serum (TMM 933-2206) from Friesenhahn Cave, Texas, which was borrowed for comparative purposes. NMC 7758 averages 8% smaller than TMM 933-2206.

Features shared by NMC 7758 and TMM 933-2206 that seem to be characteristic of *Homotherium serum* humeri, but which are not evident on humeri of *Smilodon* (UCMP 28154) and *Panthera leo atrox* (NMC 11706) are:

- (a) structural slenderness and lightness, seen particularly in the narrowness and shallowness of the shaft: sabertooth cat and American lion humeri are more robust, especially in midshaft depth; (b) the gradual meeting (the angle of juncture is more acute) of deltoid and median ridges, which occurs relatively higher on the anterior surface of the shaft. Also, the surface between the converging ridges is bevelled inward rather than outward as in the sabertooth cat and American lion;
- (c) the relative straightness of the lateral condyloid crest when viewed from behind, compared to its slight convexity in the sabertooth cat and American lion;
- (d) the slip of bone enclosing the entepicondylar foramen is situated closer to the anterior surface of the humerus than in the sabertooth cat and American lion;
- (e) the apparent prominence of the lateral epicondyle and the poorer development of the muscle scar above it,

compared to those features in the sabertooth cat and American lion. However, a larger series of humeri of each species would probably show more variability in some of these features. Recent breaks on NMC 7758 show that the interior bone of the humerus is quite fresh in appearance. The specimen is probably of late Wisconsin age.

The history of NMC 7758 is interesting. It was purchased by D.D. Cairnes in 1911 for the Geological Survey of Canada. It is part of a larger collection of Yukon Pleistocene mammals comprising the following species: *Mammuthus primigenius* (woolly mammoth), *Equus (Asinus) lambei* (Yukon wild ass), *Rangifer tarandus* (caribou), *Ovis ?dalli* (Dall sheep) and *Bison crassicornis* (large-horned bison). An entry in L.M. Lambe's original catalog states that the material came from "NO. 1 {claim}, Discovery Pass {Pup?}, Last Chance Creek, Yukon, all about 35 feet {10.7 m} from the surface and within a distance up and down the creek of 50' {15.2 m}." Lambe misidentified the specimen as the distal end of the right humerus of a deer, and it was displayed for many years in the National Museum of Canada as "Humerus of Deer".

Discussion

In summary, the American scimitar cat is known

from both Dawson and Old Crow areas of the Yukon Territory. Deeply stained specimens from the latter area suggest that the species lived in the Yukon prior to the late Wisconsin glaciation, while the Dawson specimen indicates that it survived there until late Wisconsin time. The species probably lived in central Alaska during the late Pleistocene, but the Alaskan fossils have not yet been described.

This species or a closely related form occurs in middle Pleistocene faunas of Irvington, California, Inglis IA, Florida, and Gililand, Texas. Evidently the American scimitar cat was widespread in the late Pleistocene, for there are records from Oregon, Kansas, Tennessee, Oklahoma and Texas, in addition to the Yukon and probably Alaska. Although widespread, it seems to have been a relatively rare carnivore in the North American Pleistocene. Yet, an extremely interesting concentration of material has been preserved in Friesenhahn Cave, Texas.

The evolution and dispersal history of the American scimitar cat are difficult to understand, because it has various possible derivations. The following scheme is put forward as a hypothesis for testing. *Nimravus* of

the early Miocene (Arikareean) of North America, having scimitar teeth (i.e. highly flattened, sharp upper canines rather than the rounder, longer "dirk" teeth of the sabertooth cats such as *Smilodon*), but lacking anterior flanges on the mandible, may have been ancestral to *Machairodus*, which appears to be a good generalized ancestor for the Pleistocene scimitar cats of the genus *Homotherium*. *Machairodus* occurred in the Pliocene of North America, Eurasia and Africa, and was characterized by scimitar teeth, and sometimes by anterior flanges on the mandible.

There seems to have been a primary radiation of *Homotherium* during the earliest Pleistocene from an advanced *Machairodus* stock in either North America or Eurasia, which led to a dominance of the greater scimitar cat, *Homotherium sainzelli* (= *Epimachairodus crenatidens* or *Homotherium crenatidens*), in Europe from Villafranchian to Waalian (?Nebraskan) time, and of *Ischyrosmilus johnstoni* in the early Pleistocene of North America. I stress the point that *Ischyrosmilus* and *Homotherium* are probably congeneric and that *I. johnstoni* could even be a junior synonym of *H. sainzelli*. Both were long-limbed rather slender animals with deep, massive mandibles. The relatively short, flattened scimitars and high narrow

carnassials are similar. There are many points of resemblance in the crania, including the form of the mastoid process, the shape of the auditory bulla, the keel and depressions of the basioccipital and the division of the sagittal crest (Mawby 1965, p. 584). Evidently *H. sainzelli* gave rise to a more advanced group of scimitar cats (*H. latidens*) during late Günz (?late Nebraskan) time in Europe. They were characterized by scimitar teeth and small to medium-sized mandibular flanges like *H. sainzelli* and *Ischyrosmilus*, and spread rapidly about Kansan time to Java (*H. zwierzyckii*: Djetis beds), China (*H. ultimum*: Choukoutien) and via the Bering Isthmus to North America (*H. serum*). The main difference between the earlier and later scimitar cats seems to have been the smaller size of the scimitars in the latter group (Kurtén 1968, p. 76).

I follow Kurtén (1968, p. 76) in emphasizing the great similarity between *H. latidens* of Europe and *H. serum* of North America. Certainly their mandibular dimensions are close. *H. latidens* survived in England until the last glaciation and *H. serum* lived in North America until the late Wisconsin. Undoubtedly the ultimate extinction of the scimitar cats followed the extinction

of the large prey, such as mammoths, that they were specialized in hunting.

Homotherium serum was widely distributed in North America from Kansan to Wisconsin time, ranging from Atlantic to Pacific in the United States and from Texas to the northern Yukon Territory. The American scimitar cat was the size of a lion, being characterized by long, powerful forelimbs, weaker hind limbs (Mawby 1965, p. 585), and a bob-tail like the lynx. Its "scimitars" were short compared to *Smilodon*, greatly flattened and razor-sharp.

Mazák (1970, p. 360) argues persuasively that a stone statuette about 16 cm long from upper Aurignacian deposits (approximately late Wisconsin, see Bordes 1968, Figure 73) in the cave of Isturitz in southern France depicts the lesser scimitar cat, *Homotherium latidens*, which, as has been mentioned, was probably very similar to the American scimitar cat. The head is big and the lower jaw is deep in the area of the flange, the body is short and powerful, the legs are strong (unfortunately the extremities are missing) and the tail is short and stump-like. A scaled-down outline of the skull of *H. latidens* fits remarkably well within the form of the

head of the Isturitz statuette (Mazak 1970, Figures 2, 3). Other features such as the well developed upper legs and short body and short tail also fit what is known of the scimitar cat skeleton. According to the statuette, the scimitars of *Homotherium* were hidden by the lower lip when its mouth was closed and did not bite outside the lower lip.

The American scimitar cat seems to have had no particular physical geographical habitat preference, as can be seen from its broad distribution. Perhaps its main requirement was the presence of slow-moving, thick-skinned prey like mammoths, mastodons and ground sloths. Numerous skeletons of American scimitar cats of all ages, including cubs, found in late Wisconsin deposits of Friesenhahn Cave, Texas, show that caves were sometimes used as dens (Meade 1961, p. 27). Evans (1961, p. 19) mentions that more than 441 isolated teeth of young mammoths were found in the cave, compared to only 14 of adults, indicating that scimitar cats concentrated on killing young Pleistocene elephants, often dragging them into the cave afterward. American mastodon (*Mammut americanum*) remains are also present in the cave: again, they are almost entirely young individuals. Presumably the attack of the scimitar cats would have involved

stalking the young elephants, a quick pounce, powerful forelegs clinging tightly to the prey and razor-like scimitars slashing vital parts. Attacks may have been made at dusk. Like the American lion, the American scimitar cat probably had few predators.

Family Phocidae

Phoca cf. (*Pusa*) *hispida* (ringed seal)

In 1973 on the western margin of Pauline Cove, Herschel Island, I collected a seal bone approximately 15 feet (4.6 m) above sea level in addition to marine mollusc shells (a complete pelecypod and part of a coiled shell were collected) and wood. All of these specimens are deeply iron-stained. Careful examination of the exposure revealed that the bone, shells and wood had almost certainly been derived from an oxidized organic layer 30 feet (9.1 m) above sea level. The bank at that point was approximately twice that high. The sediments in the lower half of the section are mainly sandy silt and appear to be a sequence of coastal marine deposits. I suspect that the organic sediments are of Sangamon interglacial age, but much more stratigraphic work is required before sound conclusions can be reached on this subject.

V. Rampton (personal communication 1976), who has studied

the stratigraphy of the island and the region, suggests a pre- early Wisconsin interglacial age for these organic sediments.

Referred specimen

NMC 25149 from Herschel Island Locality 5 is the base of a left scapula of a small seal. Although only 45 mm of bone is preserved distal to the glenoid cavity, and the spine is damaged, the positions of the remaining features and the size of the fossil are closely comparable with those of scapulae of the ringed seal, *Phoca (Pusa) hispida*, which presently lives in the area. Because the specimen is rather incomplete it seems best to refer it to *Phoca* cf. (*Pusa*) *hispida*. Maximum length and width measurements at the "neck" of the scapula are 20.2 mm long x 11.8 mm wide.

Discussion

Ringed seal remains found on Baillie Islands, Northwest Territories, about 250 miles (402 km) to the east of Pauline Cove, could range in age from Pleistocene to Recent (Harrington 1971a, p. 82). Bones of this species were also collected from raised beach deposits near Alert on northern Ellesmere Island. Presumably they are of postglacial age. A relatively complete skeleton of a ringed seal was excavated *in situ* near Hull, Quebec in deposits of Champlain Sea age (perhaps 11,000 years

old) (Harington and Sergeant 1972).

The following summary of the origins and dispersal history of the ringed seal is mainly based on recent work by Repenning *et al.* (1976 MS. p. 35). Marine mammals including the ringed seal have been reported from various Pleistocene strata in western Alaska. Some are from beach deposits of apparent Sangamon interglacial age, which are raised well above present sea level.

Some Paratethyan seals of 10 to 13 million years ago, such as *Phoca pontica* and *P. pannonica*, are similar to living seals of the subgenus *Pusa*. Recently discovered material of *Phoca pontica* supports the suggestion that this type of seal was ancestral to *Pusa*. The distribution of the three living species is difficult to explain zoogeographically. *Phoca (Pusa) caspica* lives in the Caspian Sea, a remnant of Paratethys, supporting further the ancestral position of *Phoca pontica*. *Phoca (Pusa) sibirica* lives in Lake Baikal in central Asia, whereas *Phoca (Pusa) hispida* occupies the Arctic Ocean, extending into the North Pacific and North Atlantic, including the Baltic Sea and lakes Saimaa and Ladoga. In Canada, ringed seals have adapted to living in freshwater in Netilling Lake,

Baffin Island. A definite trend is the adaptation of this group to cooler waters, which enabled it to disperse northward. Most likely *Pusa* moved into the Arctic Ocean about 3 million years ago.

At present, the ringed seal is the commonest and most widely distributed arctic seal. It is the smallest of the pinnipeds averaging only 4.5 feet (1.4 m) in length. Adults have dark coats with a pattern of white rings, which accounts for the specific name. Ringed seals are found wherever there is suitable land-fast ice for breeding, and they are good paleoenvironmental indicators of such conditions. During the winter they maintain breathing holes under the ice. Young are born on the fast ice in a den which the females hollow out in the snow over breathing holes, and most pups are born near the beginning of April (Mansfield 1967, p. 21). The shrimp-like crustaceans *Parathemisto* and *Mysis* are the most important food of the ringed seal, and it is interesting to note that the geographical ranges of *Parathemisto* and the ringed seal virtually coincide (Harrington and Sergeant 1972, p. 1047). This species is most important to the Eskimo economy. It is heavily hunted by man for pelts and food.

Order Proboscidea

Family Mammutidae

Mammut americanum (American mastodon)

The first record of the American mastodon from Yukon Pleistocene deposits was a molar tooth received by Tyrrell in 1902 from Gold Run Creek near Dawson. Obalski (1904, p. 216) saw mastodon remains in the Dawson Area. Although Maddren (1907, p. 7) considered Obalski's observation to be incorrect, Gilmore (1908, p. 30) stated that there were two definite records from branches of the Indian River. Other specimens from both Dawson and Old Crow areas have been found since. They include six nearly complete molar teeth (Figure 53A-B, Table 56) and several tooth fragments that are preserved in the National Museums of Canada collection.

Placer miners in the Dawson Area commonly use the term "mastodon" to describe remains of any fossil elephant. This can give people not familiar with their terminology a distorted idea of the relative abundance of mastodon to mammoth fossils recovered. According to numbers of elephant molar teeth collected in the Yukon, I estimate that less than 5% are of the American mastodon, the remainder almost entirely representing the woolly



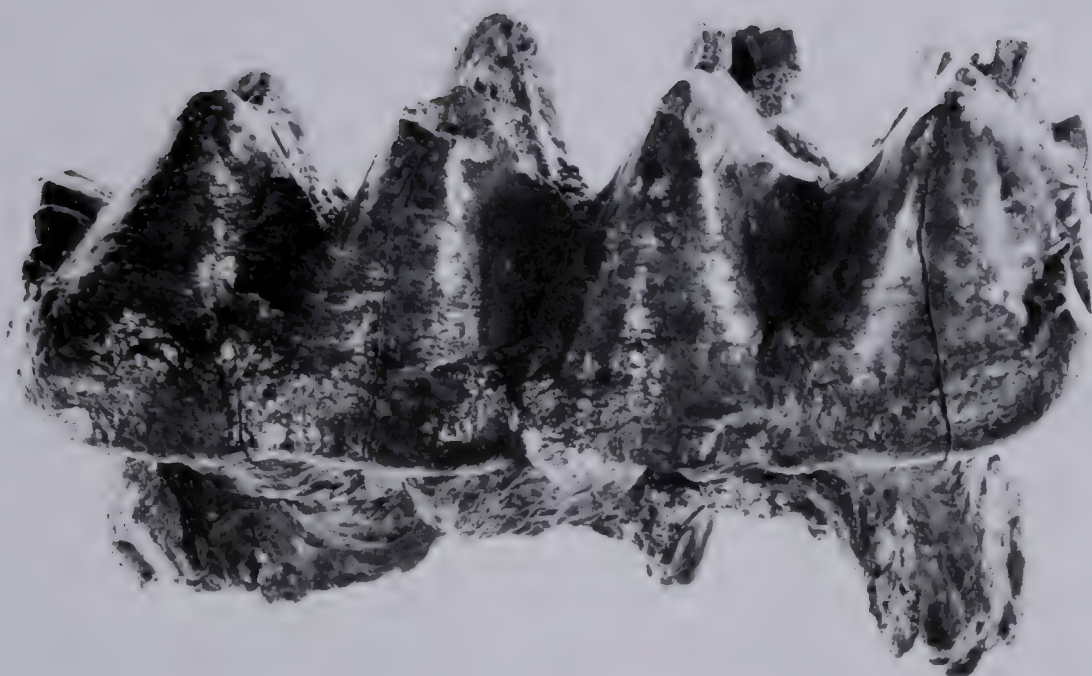
THE
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 THE
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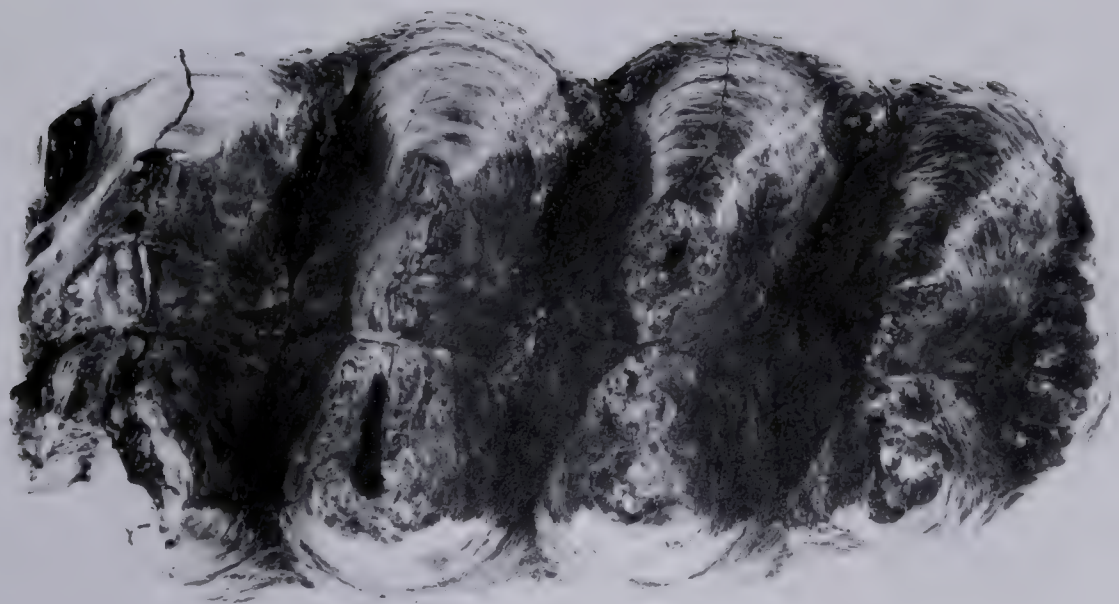
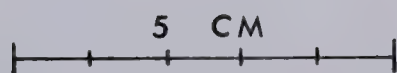
Figure 53. An RM₃ lacking most of the roots (NMC 14252, Old Crow Locality 13) of a Pleistocene American mastodon (*Mammut americanum*).

A. Lateral view (posterior of tooth is to the left).

B. Occlusal view (posterior of tooth is to the right).



A



B

Table 56. Measurements of Pleistocene American mastodon (*Mammut americanum*) molar teeth from the Yukon Territory compared to those of American mastodons from other parts of North America.

Specimens	Measurements (mm)*		
	1	2	3
<i>Mammut americanum</i> .Pleistocene			
<u>M³s</u>			
NMC 333 McQuesten Creek {River?}, Y.T.	150.0	94.8	69.2
NMC 8060 Dawson Loc. 20, Y.T.	164.3	97.0	-
AMNH 14293 Fulton, Indiana**	168.4	93.6	-
<u>M¹s</u>			
NMC 8147 Bonanza Creek, Dawson area, Y.T.	83.4	74.9	-
NMC 26601 Old Crow Loc. 11A, Y.T.	81.2	61.3	39.2
AMNH 10666 Walnut, Illinois***	86.8	75.2	-
<u>M_{3c}</u>			
NMC 14252 Old Crow Loc. 13, Y.T.	146.1	78.6	53.8 [†]
NMC 15352 Old Crow Loc. 14N, Y.T.	-	72.0 [†]	56.5
F:AM 27009 Fairbanks area, Alaska (Osborn 1936, p. 177)	187.0	101.0	-
F:AM 23335 New Mexico (Osborn 1936, p. 175)	184.0	-	-
AMNH 21920 New York (Osborn 1936, p. 175)	181.0	-	-
AMNH 2595 Shawangunk, New York (Osborn 1936, p. 175)	155.0	-	-

* 1 - Maximum length.

2 - Maximum width.

3 - Height of highest cusp from cingulum below (heavily worn teeth not measured).

** Measurements calculated from a scaled figure (Osborn 1936, p. 188, Figure 134).

*** Measurements calculated from a scaled figure (Osborn 1936, p. 173, Figure 120).

mammoth (*Mammuthus primigenius*). The American mastodon was definitely not a common element in the Yukon Pleistocene fauna, and Frick (1930, p. 77; 1933, p. 631) has noted its rarity in the Pleistocene fauna of Alaska.

Referred specimens

In 1902, J.B. Tyrrell received an RM_3 (USNM 5101, not 5102 as published by Gilmore in 1908) that had been collected beneath 25 feet (7.6 m) of muck and gravel on claim 14, Gold Run Creek (Dawson Locality 33). Tyrrell sent the specimen to W.H. Osgood for examination and it was ultimately deposited in the Smithsonian Institution. I am grateful to C.E. Ray for checking the identification of this specimen (Harington and Clulow 1973, p. 701).

NMC 8060 is a nearly complete, but heavily eroded RM^3 , which was collected on Sulphur Creek (Dawson Locality 20) by D.D. Cairnes. The margins of the posterior lophs are lacking and a well developed conelet is seen on the medial side of the valley between the metaloph and tritoloph (for terminology see Osborn 1936, p. 141).

NMC 13717 from Old Crow Locality 11A is from the anterointernal region of RM^3 . Medial parts of the well worn protolophs are preserved. The enamel is black, while the roots are dark brown. NMC 28004 from Old Crow

Locality 66 is a small part of the anterior surface of the crown of RM^3 . It is stained dark brown. M^3 s from the Yukon compare closely in shape and size with the M^3 of an American mastodon from Fulton, Indiana (AMNH 14293).

In 1933, H.S. Bostock collected a complete LM^3 (NMC 8707) from the junction of Independence and Hunker creeks (Dawson Locality 11). It was found beneath 60 feet (18.3 m) of frozen muck overlying gold-bearing gravels. The specimen is currently on display and is not available for measurement.

NMC 333, from an unspecified locality on McQuesten Creek {River?} south of Dawson, is a nearly complete LM^3 that was collected by D.D. Cairnes in 1913 (Lambe 1914, p. 299). The lophs show very little wear. In the medial side of the valley between the protoloph and metaloph is a patch of cementum-like material. R.A.A. Johnston (Lambe 1914, p. 299), who analyzed the substance, said it consisted of struvite (a hydrous phosphate of ammonium and magnesium) intermixed with small quantities of organic matter. A series of at least nine ridges girdling the roots of this tooth appear to be annular rings. It may be profitable to section and stain a series of roots of American mastodon

molars in an effort to obtain an idea of the longevity of these animals. Of course the number of the particular tooth that was sectioned would have to be considered in relation to its number in the replacement sequence.

The crown of NMC 333 is buff, while the roots are stained dark brown. NMC 23240 from Old Crow Locality 42 is a fragment from the anterior surface of the crown of LM³. It is stained black.

NMC 26601 from Old Crow Locality 11A is a nearly complete LM¹ with slightly worn cusps. The posterointernal margin of the tooth is damaged. The specimen closely matches the same tooth of an American mastodon illustrated by Warren (1852, Plate VI). It is black, suggesting a pre- late Wisconsin age. NMC 8147 from Bonanza Creek near Dawson is a nearly complete, heavily worn LM¹. The tooth is colored buff with oxidized patches.

NMC 11697 from Dawson Locality 19 is a badly damaged LM₃. Most of the protolophids and the internal metalophid are lacking. The roots are long, showing more than 20 rings from the cingulum to a point near the base. Most of the enamel on the crown is black.

NMC 14252 from Old Crow Locality 13 is an RM₃.

The tips of four of the lophids are damaged, the remainder being moderately worn. The small pentalophid is serrate. The roots are almost entirely missing. The specimen is stained dark brown. NMC 15352 from Old Crow Locality 14N is an RM_3 . Most of the roots and the protolophids and the tip of the lateral metalophid are broken off. Wear is slight on the surface of the complete lophids. The pentalophid is poorly developed. "Struvite" is seen in the valleys of the molar.

NMC 29267 from Old Crow Locality 44 is an RM_3 lacking most of the protolophids and the lateral metalophid. It measures 72.6 mm across the tritolophids. The enamel is mottled grayish black and the roots are brown. The fossil was collected by W.N. Irving 3 m above stream level, and although it was not definitely in place, I suspect that it was derived from Unit 2 and that it may be of ?Sangamon interglacial age. Unit 2 marks a time of spruce invasion and probably warmer, wetter climate - conditions that would be suitable for mastodons.

Discussion

It seems that most of the American mastodon remains from the Old Crow Basin are of pre- late Wisconsin age. One partial molar may have been derived from ?Sangamon deposits. Fossils from the Dawson Area have

a relatively fresh appearance compared to those from the Old Crow Area, suggesting that they may have survived in the former place until the late Wisconsin. None of the specimens from the Yukon - Alaska region has been radiocarbon dated.

In Alaska, mastodon remains have been recovered from sediments at Cripple Creek sump near Fairbanks that are considered by Péwé (Péwé and Hopkins 1968, p. 269) to be of Illinoian age. I suggest that this material is of early or late Illinoian age, as spruce forest, to which this species seems best adapted, would have been scarce in central Alaska during the peak of the Illinoian glaciation (Péwé 1975a, p. 84; 1975b, p. 12). Perhaps the best specimen from Eastern Beringia comprises a partial mandible with teeth, an upper tusk, both radii, ulnae, forefoot bones and the distal end of a femur from an individual mastodon. It was collected from deposits of possible Wisconsin age near Fairbanks (Frick 1933, pp. 631-632; Osborn 1936, pp. 176-177).

In Canada, most mastodons (over 60 specimens) have been found in postglacial deposits of southern Ontario. Scattered teeth have been recovered from Nova Scotia and New Brunswick, and a nearly complete

skeleton was collected near Hillsborough in the latter province. Farther west, mastodon teeth have been reported from: Prince Albert, Pilot Butte, and Jansen, Saskatchewan; Edmonton, Cold Lake, Wapiti River, and possibly Pincher Creek, Alberta; Minaker River, 65 miles (105 km) north of Mile 147 on the Alaska Highway, Courtenay area, and Shawnigan Lake, British Columbia. A tooth fragment collected from Lower Carp Lake north of Yellowknife, Northwest Territories is probably of interglacial age (Harrington 1971, pp. 81-82).

Major concentrations of American mastodon remains in the United States are from the eastern half of the country and the west coast. The species evidently reached Mexico (Hibbard 1955, p. 54, Plate 2, Figure 2).

Mastodonts (*sensu* Tobien 1973, p. 57 = Mammutidae (Simpson 1945, p. 133)) evolved in the early Oligocene in Africa, migrated to Eurasia during the early Miocene and entered North America via the Bering Isthmus during the late Miocene or early Pliocene (Clarendonian). The first zygodont mastodonts entering North America at that time belonged to the genus *Miomastodon*. Evidently during the middle Pliocene in the Old World, as well as in North America, a parallel transition from a *Miomastodon* stock to more specialized zygodonts occurred, leading to

Mammut americanum, which survived in North America until postglacial time (Osborn 1936, pp. 132-133; Tobien 1973, pp. 57, 59). Among the earliest records of *Mammut* from North America are those from the late Pliocene (early Blancan) Hagerman fauna of Idaho, and the early Pleistocene (late Blancan) faunas of Blanco, Texas and Broadwater, Nebraska (Skinner *et al.* 1972, p. 129). Of 28 directly or indirectly radiocarbon-dated specimens of *Mammut americanum* from eastern North America, 80% yielded dates between 12,000 and 9,000 years B.P. (Dreimanis 1968, p. 257).

Mammut americanum was confined to North America, being rarely found in the extreme northwestern part of the continent and Mexico. It was most common in the east, where it found favorable habitat in spruce forests or open spruce woodlands that prevailed there throughout much of the Pleistocene (Dreimanis 1968, p. 257).

Obviously these elephants were able to survive in other habitats, such as pine-parkland in the Ozarks of western Missouri (King 1973, p. 560); and Martin and Guilday remark on their presence in Florida well south of the known limits of boreal forest, even during late Wisconsin time. Nevertheless, fossils of *Mammut americanum* are generally valuable as paleoenvironmental indicators of coniferous forest.

Compared to modern elephants and mammoths, American mastodons were squat and long in the body, with straighter tusks. Vestigial tusks were present in the lower jaw. A mounted skeleton from Rancho La Brea has a shoulder height of only 1.9 m (Stock 1965, p. 49). One of the largest mastodons known, the Warren mastodon from New York, was about 2.6 m high at the shoulder (Osborn 1936, p. 179). Mastodons had reddish brown hair. Judge Miller, in describing the discovery and appearance of a skeleton at Shawangunk, New York stated that, - 'around and in the immediate vicinity were locks and tufts of hair of a dun brown, of an inch and a half to two inches and a half long and, in some instances, from four to seven inches in length' (Scott 1962, p. 281). No mention is made of underwool, so presumably American mastodons were not so well adapted to cold tundra climate as were woolly mammoths (*Mammuthus primigenius*).

A glimpse of the American mastodon as it appeared to Paleo-Indians may be gained by looking at the figure of an elephant incised on the surface of a large whelk shell found in a layer of peat near Holly Oak, Delaware. It was collected in 1864 by H.T. Cresson, and was evidently used as a pendant, as two holes bored in one end indicate. The engraving shows a long, squat

elephant with a good deal of hair and relatively short, straight tusks. It has been interpreted previously as a mammoth (Meggers 1972, p. 14; Kraft and Thomas 1976, p. 756), but I consider that unlikely. The length of the body from base of neck to base of tail is approximately the same as the length from the top of the back to the feet, which corresponds almost exactly to the proportions of the Warren mastodon (Osborn 1936, Figure 124). In comparison the length of the body in a Columbian mammoth (*Mammuthus columbi* = "*Parelephas jeffersonii*", AMNH 9950) reaches (in relative vertical height) only from the top of the back to the distal end of the humerus (Osborn 1942, Figure 931). The elephant depicted on the pendant lacks the pronounced "knob" on the top of the skull, the steeply slanting back and the highly curving tusks of woolly mammoths engraved by Paleolithic artists on the walls of Les Combarelles (Augusta and Burian 1963, Plate 15) and Rouffignac (Ucko and Rosenfeld 1967, Figures 13, 30). In addition, I suggest that it would be more natural for Paleo-Indians to see mastodons in a moist peaty area of the northeastern United States than mammoths. It is worth noting that among many artifacts and other remains collected in the same area by Cresson and his associates was a mastodon tooth (Kraft and Thomas 1976, p. 756).

Of nine well-preserved American mastodons from New Jersey, New York, Virginia and Ohio, two had food in the mouth (twigs of larch, and resins and tars with a high percentage of spruce pollen and some of pine, grass and composites), and the remainder had stomach contents found within their rib cages - the material consisted of: hemlock and cedar wood, conifer twigs, swamp plants including reeds, and mosses (Dreimanis 1968, Table 2). Seven bushels (247 liters) of plant material evidently composed the stomach contents of a mastodon found at Hackettstown, New Jersey (Hay 1923b, p. 67).

There is good evidence from Friesenhahn Cave, Texas that American scimitar cats (*Homotherium serum*) preyed on young mastodons. Probably sabertooth cats (*Smilodon*) also hunted them. Despite abundant finds of American mastodon remains in late Wisconsin deposits, sites where they have been killed by man are virtually unknown (MacDonald 1971, p. 36).

Family Elephantidae

Mammuthus meridionalis (southern mammoth)

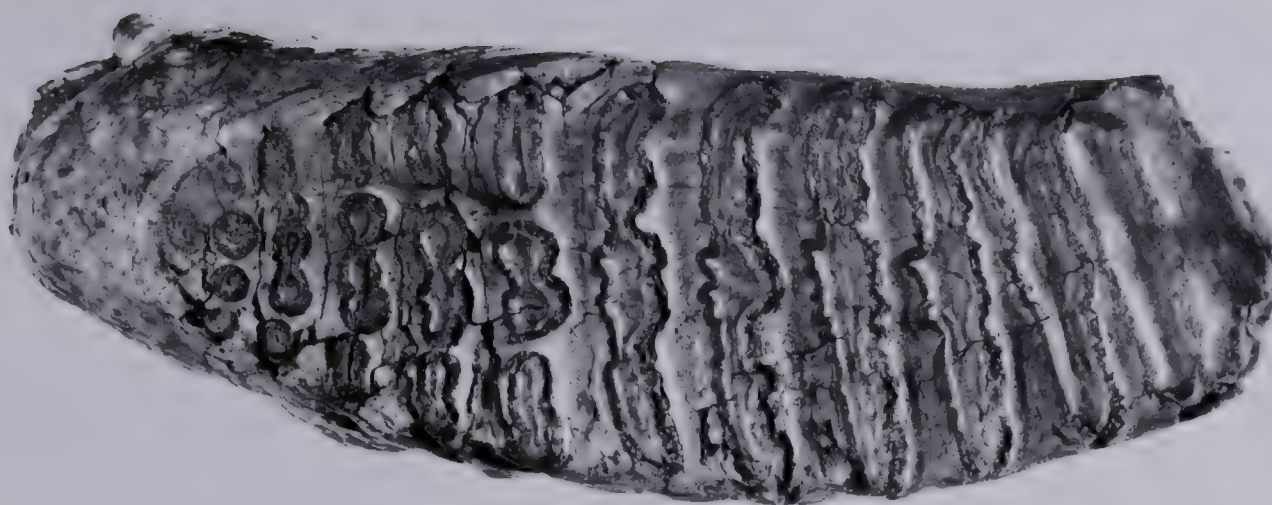
Among hundreds of woolly mammoth (*Mammuthus primigenius*) teeth are a few belonging to more primitive

forms. Five well preserved molars (Figures 54A-B, 55A-B, Table 57) from Pleistocene deposits on the Old Crow and Porcupine rivers are best referred to the most progressive stage (Bacton Stage) of the southern mammoth. This species has been reported previously from early to middle Pleistocene sediments in southern North America (Maglio 1973, p. 62), but never before from the north-western part of the continent, through which they must have passed in their dispersal from Eurasia.

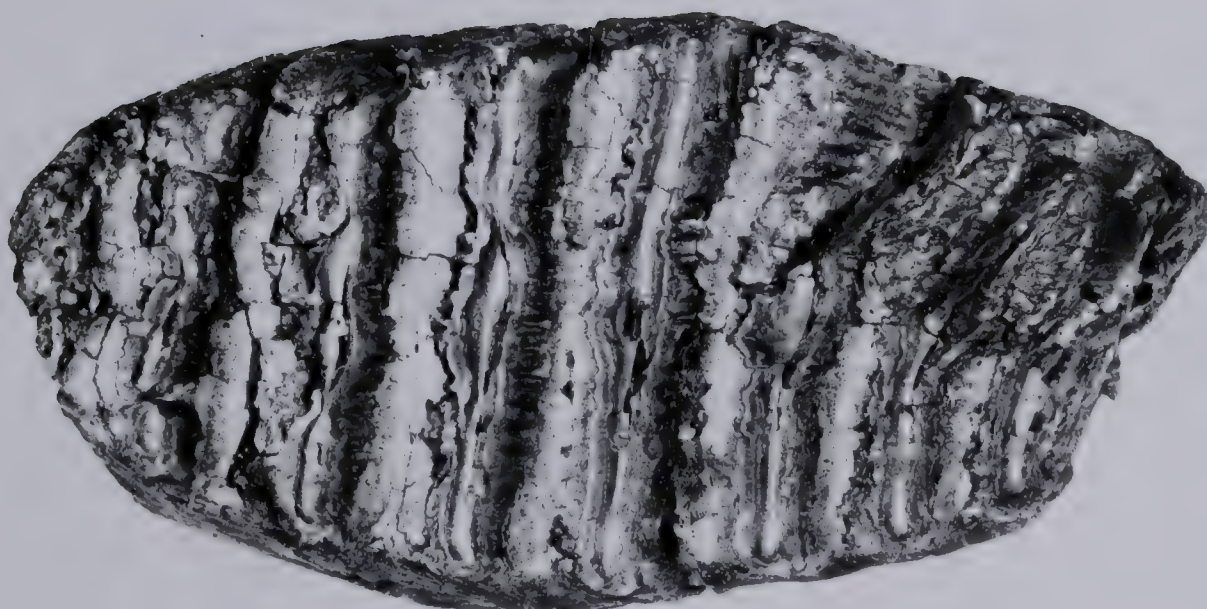
Measurements on mammoth teeth are often difficult to replicate, so in studying this group, I have confined myself to description of some of the more complete lower molars (particularly M_3 s) which are most commonly used for taxonomic purposes, and for which Maglio (1973, pp. 8-13) has established clear, standardized metrical procedures and comparative tables. Of the measurements given, I consider the following ones most significant: total number of enamel plates (lamellae); lamellar frequency (the number of plate-cement units within a 100 mm interval); and enamel thickness. These characters are functionally important in the adaptation of mammoths to particular habitats, and have changed rather rapidly throughout the Pleistocene, providing a broadly useful biostratigraphic key.



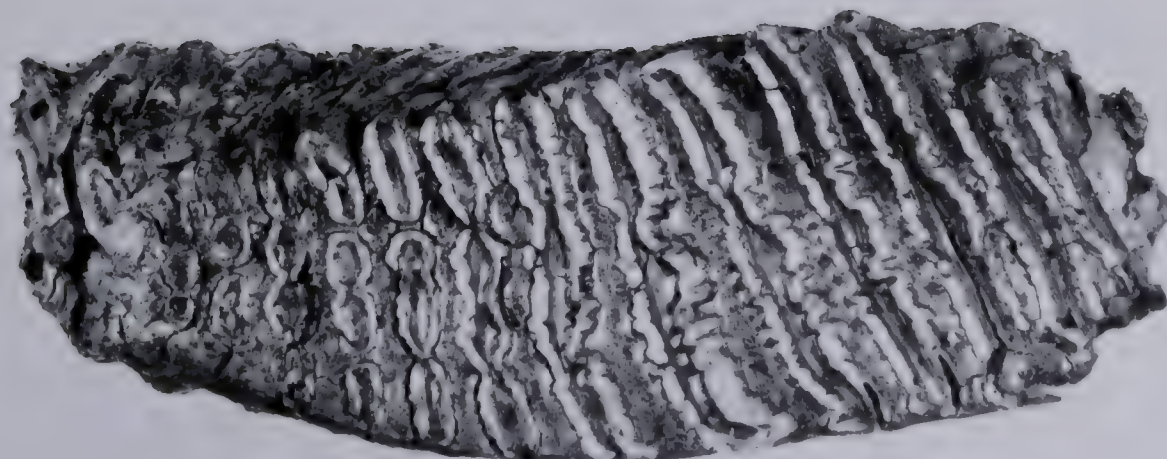
Figure 54. A. Occlusal view of an LM_3 (NMC 14509, Old Crow Locality 22) of a Pleistocene southern mammoth (*Mammuthus meridionalis*).
B. Occlusal view of an LM_1 (NMC 13736, Old Crow Locality 11A) of a Pleistocene southern mammoth (*Mammuthus meridionalis*).
C. Occlusal view of an LM_3 (NMC 21013, Old Crow Locality 7) of a Pleistocene steppe mammoth (*Mammuthus* cf. *armeniacus*).



A



B



C



Figure 55. Compare with Figure 54.

- A. Medial view of NMC 14509.
- B. Medial view of NMC 13736.
- C. Medial view of NMC 21013.

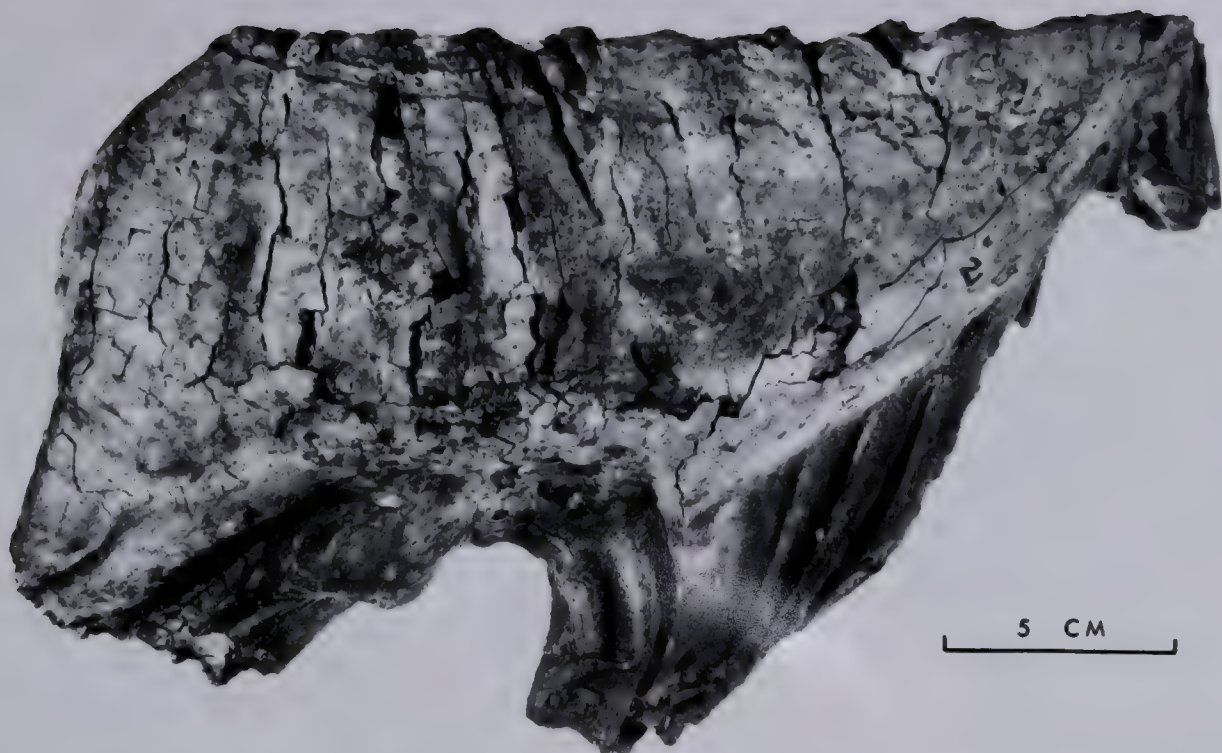


Table 57. Measurements of Pleistocene southern mammoth (*Mammuthus meridionalis*) molar teeth from the Yukon Territory compared to those of southern mammoths from Eurasia and North America.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
M₃^s							
<i>Mammuthus meridionalis</i> .Pleistocene, Y.T.							
NMC 14509 Old Crow Loc. 20	14e	263.9	89.2	103.0	5.0	2.8	115.5
NMC 17061 Porcupine Loc. 100	14	234.7	73.8	70.9	5.0	2.8	96.1
<i>Mammuthus meridionalis</i> .Pleistocene, Eurasia (Maglio 1973, Table 30)							
M	12.1	266.3	97.2	115.0	4.6	3.4	126.4
OR	10.0- 14	212.0- 306.0	69.1- 119.4	75.0- 152.0	3.5- 5.9	2.4- 4.1	107.8- 165.5
N	19	18	36	17	36	33	14
SD	1.5	27.5	12.4	21.0	0.6	0.4	15.4
V	12.3	10.3	12.8	18.3	12.8	12.0	12.1
<i>Mammuthus meridionalis</i> .Pleistocene, Nebraska (Osborn, 1942, p. 1035)							
CMNH 1359 Angus	14	289.0	84.0	-	5.5	-	-
M₂^s							
<i>Mammuthus meridionalis</i> .Pleistocene, Y.T.							
NMC 15540 Old Crow Loc. 20	10e	158.0 ⁺	74.2	98.2	6.0	2.4	132.4
<i>Mammuthus meridionalis</i> .Pleistocene, Eurasia (Maglio, Table 30)							
M	9.3	198.7	85.1	97.8	5.1	2.8	121.6
OR	8.0- 10.0	190.0- 209.0	69.0- 97.0	90.9- 111.2	4.6- 6.1	2.4- 3.5	104.6- 141.4
N	6	3	10	5	10	8	5
SD	0.8	9.6	7.9	8.0	0.4	0.4	16.7
V	8.7	4.8	9.2	8.1	8.2	13.9	13.8
M₁^s							
<i>Mammuthus meridionalis</i> .Pleistocene, Y.T.							
NMC 13736 Old Crow Loc. 11A	10e	143.0 ⁺	70.7	90.6	6.0	2.2	128.2
NMC 20424 Old Crow Loc. 22	10e	153.8 ⁺	69.9	74.3 ⁺	5.5	2.3	-
<i>Mammuthus meridionalis</i> .Pleistocene, Eurasia (Maglio, Table 30)							
M	9.2	151.6	67.0	94.0	7.0	2.2	120.1
OR	8.0- 10.0	116.8- 185.0	53.5- 73.4	93.1- 94.9	6.6- 7.7	1.9- 2.6	129.4- 130.8
N	4	4	4	2	4	4	2

* Measurements follow those of Maglio (1973).

- 1 - Plate (lamella) number.
2 - Length.
3 - Width.
4 - Height.

- 5 - Lamellar frequency (number of plate-
cement units in a 100 mm interval).
6 - Enamel thickness (average).
7 - Hypsodonty index ($\frac{H}{W} \times 100$).

Referred specimens

NMC 14509 from Old Crow Locality 22 is an LM₃ lacking the ends of the roots. Thirteen of an estimated 14 enamel plates were in wear when the individual represented by the fossil died. The enamel is thick and slightly wrinkled and the plates are widely separated. Among North American mammoth molars figured by Osborn (1942), it appears to be closest to *M. meridionalis* from Nebraska (= "*Archidiskodon meridionalis nebrascensis*"; CMNH 1359), which Lugen and Schultz considered to be of Yarmouth interglacial age (Osborn 1942, p. 1033). The Nebraska specimen also has slightly wrinkled enamel. NMC 14509 is stained brown and has black enamel.

NMC 17061 from Porcupine Locality 100 is a highly oxidized LM₃ lacking the ends of the roots. Most of the first enamel plate has broken away. Of a total of 14 enamel plates, all are in wear, denoting an old individual. The enamel is thick and the plates are widely spaced as in NMC 14509, but wrinkling of the enamel is finer. The relative primitiveness of this molar and signs that it had been covered by highly oxidized matrix suggest to me that the fossil could have been derived from the basal interglacial unit at Porcupine Locality 100, which I consider to be of Yarmouth or earlier interglacial age. Hopefully, mammoth teeth will be found *in situ* at

this exposure in the future. The tooth is rusty brown with black enamel. Probably both NMC 14509 and 17061 would have had slightly thinner enamel measurements and slightly higher lamellar frequency readings if they had not been so heavily worn. In any case, the following M_2 and M_1 specimens tend to confirm the presence of southern mammoths in the northern Yukon Territory during the Pleistocene.

NMC 15540 from Old Crow Locality 20 is an RM_2 lacking the ends of the roots. I estimate that it had 10 plates, all of which were being worn when the animal died. Probably two anterior plates are missing and the occlusal surface of the seventh is damaged. The enamel is thick and has a few coarse plications. The tooth is dark brown with thick, black enamel.

NMC 13736 from Old Crow Locality 11A is a moderately worn LM_1 lacking the tips of the roots. Of a total of 10 enamel plates, all are worn but the posteriormost. The anterior of the specimen, particularly the lateral part, and the posterior of the tooth have been damaged. The molar is characterized by thick enamel and widely separated plates. It is deeply oxidized, approaching a reddish-brown color, and has black, finely wrinkled enamel.

Traces of indurated medium sand matrix are cemented to the lateral surface of the roots.

NMC 20424 from Old Crow Locality 22 is an LM₁, with relatively thick surrounding cementum. The roots are lacking, and I estimate that two anterior plates are missing. The posterior part of the tooth is slightly damaged. The enamel plates are comparatively thick, having extensive "lakes" of dentine. Of an estimated total of 10 plates, all are worn. The specimen is rust to brown in color with grayish-black enamel.

Discussion

The dark staining of the Yukon specimens indicates their probable pre- late Wisconsin age, and their primitive morphological characteristics suggest an early to middle Pleistocene age. Unfortunately, none was found in place, although NMC 17061 may have been derived from the oxidized deposits of ?Yarmouth or earlier interglacial age at Porcupine Locality 100. Perhaps *Mammuthus meridionalis* would have been comfortable during that period in the northern Yukon in an environment with affinities to a boreal forest - aspen parkland margin, where forest cover (spruce, birch, pine and sporadic hazel), and open heath areas may have been common (Lichti-Federovich 1974, p. 4). These fossils are more primitive from an evolutionary viewpoint than

mammoth teeth from the Mindel (?Kansan) Olyor Suite of the Kolmya Lowland in Siberia, for Sher (1971) indicates that an M_3 (GIN 835-214/27) has 22-23 enamel plates with a lamellar frequency averaging 7, and an enamel thickness of 1.8-2.5 mm. In my opinion, those characteristics best fit *Mammuthus armeniacus*.

Although no fossils of the southern mammoth have yet been recorded from Alaska, undoubtedly the species lived there once. *Mammuthus* cf. *meridionalis* (= "*Mammuthus* cf. *haroldcooki*") has been recorded from late Aftonian interglacial deposits at Wellsch Valley, Saskatchewan, and *M. meridionalis* (= "*Mammuthus imperator haroldcooki*") is known from Kansan age sediments at Medicine Hat, Alberta (Stalker and Churcher 1972, Tables 2, 3).

Mammuthus had its origins in sub-Saharan Africa, being part of an early Pliocene radiation of the Elephantinae on that continent. *M. subplanifrons*, the earliest known species, spread rapidly into eastern and southern Africa. By the late Pliocene, a more progressive species (*M. africanavus*) began moving northward, simultaneously giving way to emerging populations of *Loxodonta* and *Elephas* in sub-Saharan Africa. In the early Villafranchian, the *M. africanavus* stock that gave

rise to the southern mammoth had entered southern Europe, probably across the Gibraltar Isthmus. *Mammuthus meridionalis* (Laiatico Stage) is first recorded from scattered localities in Italy and the Netherlands. By the close of the Pliocene, a more progressive southern mammoth (Montavarchi Stage) had spread throughout Europe and had reached England (Maglio 1973, p.117), which was part of continental Europe then (Frenzel 1968). Thus, the trend in this group was toward better adaptation to cold climate, and exploitation of the expanding northern grasslands. The most advanced stock (Bacton Stage) of the southern mammoth had reached the Taman Peninsula in the Soviet Union during the Cromer (?Aftonian) interglacial (Kahlke 1973, p. 12), and evidently had crossed the Bering Isthmus to North America at the beginning of the Pleistocene about 2 million years ago.

Perhaps one of the earliest records in North America is from Wellsch Valley, Saskatchewan, where *M. meridionalis* may have lived about 1.7 million years ago according to paleomagnetic evidence (A. MacS Stalker, personal communication 1976). It evidently persisted on the Canadian plains until Kansan time, as indicated by material from Medicine Hat, Alberta. A number of specimens from Idaho, Kansas, Nebraska, and Oklahoma

(originally called "*Archidiskodon hayi*", "*Archidiskodon haroldcooki*", and "*Archidiskodon meridionalis nebrascensis*") are among the earliest elephants known from North America. The specimen from Bruneau, Idaho is about 1.36 million years old according to potassium-argon dates (Maglio 1973, pp. 61-63, 117-118).

Mammuthus meridionalis had a Holarctic distribution from Europe, where it survived from Villafranchian to Cromerian (?Aftonian) time, to North America, where it seems to have lived between Nebraskan and Kansan time. Probably the southern mammoth looked more like the modern Asiatic elephant (*Elephas maximus*) than the African species (*Loxodonta africana*). Its back was horizontal or arched, rather than sloping. The tusks were large and curved upward. Its shoulder height was approximately 3.5 to 3.7 m. A good idea of the appearance of the southern mammoth can be gained from an illustration based on a mount of the Angus, Nebraska skeleton (Osborn 1942, Figure 927). A complete skeleton from Durfort in southern France is displayed in Paris. Kurtén (1968, p. 134) considered that the southern mammoth was not highly specialized but occupied savannas, bush steppes and woodlands. It was probably not successful in arid steppe environments. Therefore, it seems to be of little use as a

paleoenvironmental indicator other than signifying moderately warm, moist conditions. The molar teeth of this species, with their widely spaced lamellae suggest that it was able to feed on succulent grasses and shrubs. Perhaps scimitar and dirk-toothed cats were among predators of the young or disabled.

Mammuthus cf. *armeniacus* (steppe mammoth)

Four lower molars from Pleistocene deposits of the Old Crow Basin, and another enclosed in most of a mandible from the Dawson Area (Figures 54C, 55C, 56, Table 58) have characteristics lying between those of the southern mammoth (*Mammuthus meridionalis*) and the woolly mammoth (*Mammuthus primigenius*). They have more enamel plates, closer lamellae and thinner enamel than *M. meridionalis*, probably indicative of a dry grassland adaptation. Two kinds of steppe mammoths with similar teeth are known: (a) those that evolved from *M. meridionalis* in the grasslands of southern North America, which are called the imperial (*M. imperator*) and the Columbian (*M. columbi columbi*, and *M. columbi jeffersoni* - a more advanced stage) mammoths; and (b) those that evolved from *M. meridionalis* in Eurasia, which are called *Mammuthus armeniacus*. I consider that the Yukon specimens



Figure 56. Restoration of a steppe mammoth
(*Mammuthus armeniacus*) as it may have
appeared in the northwestern Yukon during
a Pleistocene glacial phase. Ink sketch
by Charles Douglas.

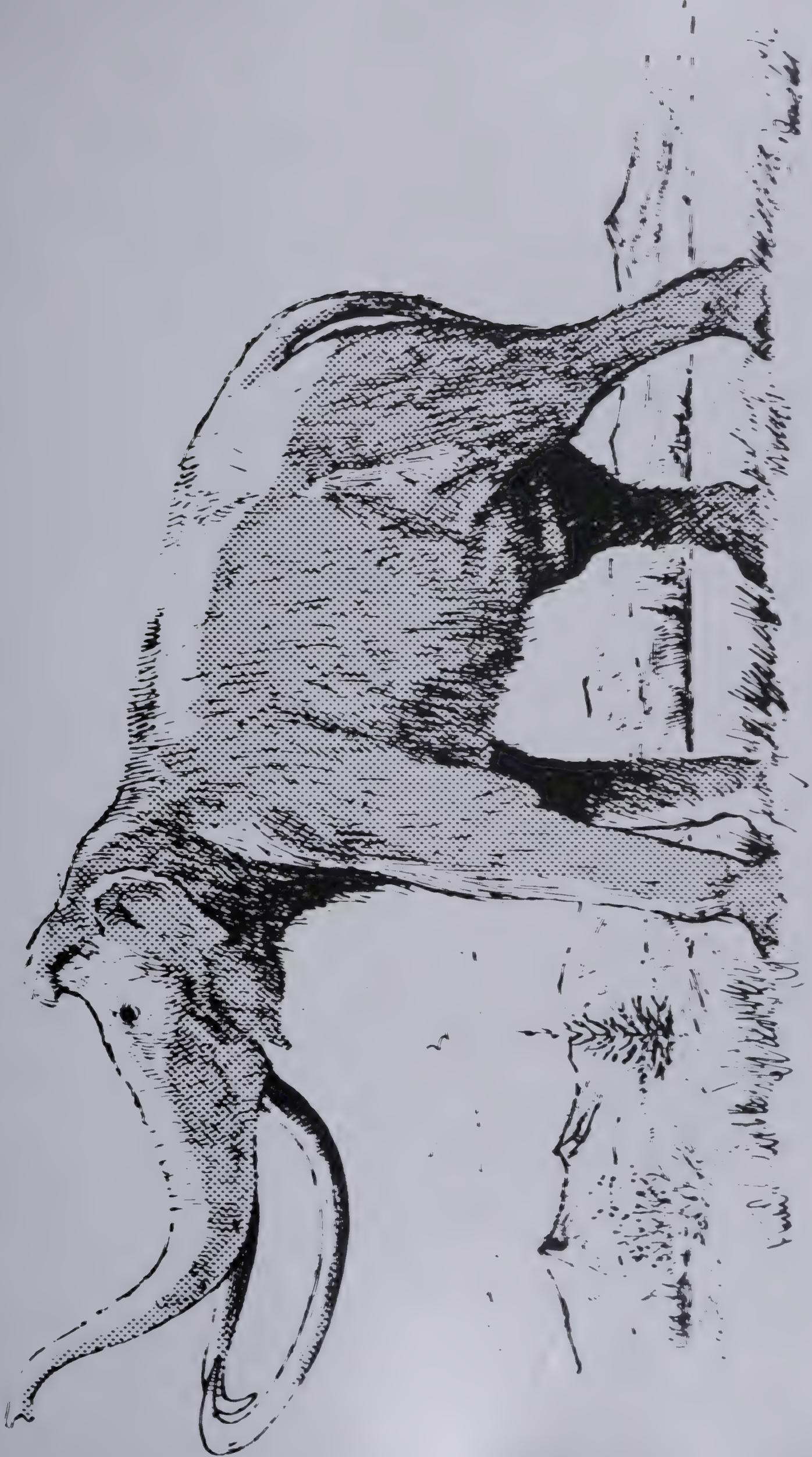


Table 58. Measurements of Pleistocene steppe mammoth (*Mammuthus* cf. *armeniacus*) M_3 s from the Yukon Territory compared to those of steppe mammoths (*Mammuthus armeniacus*) from Eurasia.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Mammuthus</i> cf. <i>armeniacus</i> . Pleistocene, Y.T.							
NMC 21013 Old Crow Loc. 7	16e	216.0 ⁺	78.6	108.6	6.0	2.3	138.2
NMC 29270 Dawson Loc. 8	16e	265.0e	94.8	-	5.0	2.2	-
NMC 20560 Old Crow Loc. 32E	9.5 ⁺ (15e)	-	82.3	79.7	6.0	2.2	96.8
NMC 13737 Old Crow - locality unknown	10 ⁺ (16e)	-	74.9	80.2	6.5	2.4	-
NMC 14029 Old Crow Loc. 5	14 ⁺ (20e)	-	120.6	118.2	6.5	1.9	97.8
<i>Mammuthus armeniacus</i> . Pleistocene, Eurasia (Maglio 1973, Table 31)							
M	18.3	298.2	87.6	139.8	6.3	2.3	165.9
OR	15.0- 21.0	236.0- 340.0	70.0- 113.0	96.0- 160.0	5.0- 7.2	1.8- 3.0	133.2- 206.6
N	15	14	21	21	22	20	16
SD	2.0	32.8	11.5	17.9	0.6	0.3	21.9
V	10.8	11.0	13.1	12.9	10.3	13.8	13.2

* Measurements follow those of Maglio (1973).

1 - Plate (lamella) number.

2 - Length.

3 - Width.

4 - Height.

5 - Lamellar frequency (number of plate-cement units in a 100 mm interval).

6 - Enamel thickness (average).

7 - Hyposodonty index ($\frac{H}{W} \times 100$).

may represent either or both of these groups and have described them as *Mammuthus* cf. *armeniacus* largely as a matter of convenience.

Unfortunately there is no authoritative study explaining how the teeth of the North American steppe mammoths differ from those of the Eurasian species. The confusion of nomenclature in the later North American mammoths is succinctly stated by Maglio (1973, p. 62). Therefore, I use the term *M. cf. armeniacus* in the broadest possible sense to describe these teeth that are transitional between those of the southern elephant and the woolly mammoth. It is a practical measure too, for Maglio (1973, Table 31) has provided a handy yardstick for comparison. The Yukon specimens fit rather well within the size limits of *M. armeniacus*, except NMC 14029, which is broader than any of 21 M_3 s sampled by Maglio. Zoogeographically, it would have been feasible for either *M. armeniacus* to migrate from Eurasia to Eastern Beringia via the Bering Isthmus in the middle Pleistocene, or for *M. imperator* and/or *M. columbi* to reach it from southern North America during a non-glacial phase or phases of the middle to late Pleistocene.

Referred specimens

NMC 21013 from Old Crow Locality 7 is an LM_3

lacking most of the roots. Of an estimated 16 enamel plates, 14 were in wear when the animal died. The first plate is broken away; most of the second and the posteriormost plates are damaged. The enamel is plicated and pearl gray in color; the remainder of the tooth is stained brown.

NMC 29270 from Dawson Locality 8 is a complete, well worn RM_3 in place in a mandible that lacks most of the right ascending ramus, and the posterior half of the left ramus. Part of the socket for LM_3 and a piece of its root are preserved. Thirteen or 14 of an estimated 16 plates are worn. The tooth and mandibular bone are fresh-looking, like other fossils of late Wisconsin age from the area. If this specimen is of Wisconsin age, then it likely represents the Columbian mammoth. I intend to have part of the mandibular bone radiocarbon dated. The enamel is whitish.

NMC 20560 from Old Crow Locality 32E is an LM_3 lacking the anterior part. Most of the roots are missing and much of the cementum has broken away from the lateral surface. Median enamel loops are clearly developed on plates 6 and 7 counting from the posteriormost one that is worn. Of an estimated total of 15 plates,

9½ are preserved. The enamel is finely wrinkled and is gray in color. The rest of the tooth is dark brown.

NMC 13737 from an unknown locality on Old Crow River is the anterior part of an RM_3 . An estimated six posterior plates are missing, and of the 10 present, the greater part of the anteriormost plate is worn away. The enamel is pearl gray and finely plicated.

NMC 14029 from Old Crow Locality 5 is an RM_3 , which has been damaged on the lateral margin of the five anterior plates. Much of the posterior portion of the tooth is missing, as are most of the roots. There may have been about 20 plates altogether: only about 14 are preserved. The tooth is remarkable for its breadth, said to be characteristic of the imperial mammoth of North America (Maglio 1973, p. 62).

Discussion

All of the Old Crow fossils are stained brown and are probably of pre- late Wisconsin age. It is interesting to note that the enamel on these specimens is paler than the black enamel of the *M. meridionalis* molars described previously. Perhaps, in this case, the degree of permineralization of the enamel is indicative of the difference between early Pleistocene and middle

to late Pleistocene teeth. The fresh appearance and relative completeness of NMC 29270 from Quartz Creek near Dawson suggests that a few steppe mammoths shared the Wisconsin arctic steppe environment with more abundant woolly mammoths. As steppe mammoths have not been reported from Alaska, these records appear to be the first for Eastern Beringia.

Mammuthus armeniacus is clearly derived from the southern mammoth *Mammuthus meridionalis*, being transitional morphologically and stratigraphically between the latter and the woolly mammoth. Among the earliest *M. armeniacus* specimens recognized are those from the Cromer Forest Bed of England and Mosbach I, Germany, which are approximately of Cromerian (?Aftonian) interglacial age. As Kurtén (1968, p. 136) has remarked: "So it is to some extent a matter of taste where the boundary between the species is drawn; what is important of course is that we have evidence of the direct emergence of the steppe mammoth by gradual transformation from a steppe race of the southern elephant." During the Mindel (?Kansan), *M. armeniacus* was a characteristic member of Eurasian middle Pleistocene faunas, and has been recorded from Spain to northeastern Siberia (Kahlke 1973). A few relatively primitive mammoth teeth

from Mindel (?Kansan) deposits in the Kolyma Lowland are best referred to this species. Certainly, these wide-ranging mammoths were not far from Eastern Beringia at that time. Early in the Riss (Illinoian) glacial the transition between *M. armeniacus* and *M. primigenius* occurred.

With regard to the North American steppe mammoths, *Mammuthus imperator* first appeared during the middle Pleistocene in the western part of the continent. It is distinguishable from its ancestor *M. meridionalis* by its greater number of molar plates and more hypsodont molars. *Mammuthus columbi* arose from *M. imperator* sometime prior to the Illinoian glaciation. It was the dominant North American mammoth of the late Pleistocene, being mainly restricted to southern North America where it was very abundant (Hibbard 1955b; Skeels 1962, p. 117). The name "*Mammuthus jeffersoni*" is sometimes applied to the more advanced type that was common on the American plains during the Sangamon and Wisconsin phases, but I prefer to consider it a northern subspecies of *M. columbi* (e.g. *M. columbi jeffersoni*) following Aguirre (1969, p. 1374). The species became extinct about 11,000 to 10,000 years ago (Harington *et al.* 1974, p. 298).

M. armeniacus ranged from Spain to Siberia, being the dominant mammoth of the Eurasian middle Pleistocene. *M. imperator* and *M. columbi* were the most common mammoths in southern North America from the middle to late Pleistocene. Any or all of these species could have reached Eastern Beringia during the Pleistocene. In size, *M. armeniacus* exceeded all other mammoths, reaching a shoulder height of 4.5 m in the largest recorded specimens. The tusks were moderately curved, extending up to 5 m in length (Kurtén 1963, p. 136). *M. columbi* was about 3.4 to 3.6 m in height. It may have had a hairy coat, considering its adaptation to cool grasslands, but there is no direct evidence on this subject. Its tusks curved gently downward, outward and inward. Data on the probable habitat of the Columbian mammoth have been summarized by Harington *et al.* (1974, pp. 298-301). Skeels (1962, p. 118) points out that *M. columbi jeffersoni* has teeth most like those of the living Asiatic elephant, which is almost exclusively a grazer. She adds that this mammoth may have supplemented its normal grass diet in winter by feeding on alder, willow and birch. Of the predators known to have occupied the Yukon during the Pleistocene, perhaps the scimitar cat (*Homotherium serum*) would have been best adapted to preying on these steppe mammoths

(Evans 1961, p. 19; Meade 1961, p. 27). Paleo-Indians hunted the Columbian mammoth (Harington *et al.* 1974, p. 298).

Mammuthus primigenius (woolly mammoth)

A sample of 9 lower molar teeth (Figure 57, Tables 59-60) have been selected to demonstrate the presence of the woolly mammoth in the Yukon Pleistocene. Specimens have been collected from many parts of the Yukon Territory including the Old Crow Area, Dawson Area, Porcupine River, Rock River, Sixtymile Area, and Herschel Island. A description of various skeletal elements of this species from Gold Run Creek (Dawson Locality 32) has been given previously (Harington and Clulow 1973, pp. 705-708).

With horse and bison, woolly mammoth fossils are among the most common from ice age deposits in the Yukon. One of the most interesting finds during the course of this study was the discovery of much of an articulated skeleton on the Whitestone River (Locality 43). The mandible of the Whitestone mammoth is on display with that of a juvenile of the same species in the National Museum of Natural Sciences in Ottawa. It



Figure 57. Occlusal view of the anterior part of a mandible containing M_3 s (NMC 17659, Whitestone Locality 43) of a Pleistocene woolly mammoth (*Mammuthus primigenius*).



Table 59. Measurements of Pleistocene woolly mammoth (*Mammuthus primigenius*) M_2 s and M_3 s from the Yukon Territory compared to a sample measured by Maglio (1973, Table 32).

Specimens		Measurements (mm)*						
		1	2	3	4	5	6	7
M_3 s								
<i>Mammuthus primigenius</i> .Pleistocene, Y.T.								
NMC 15264 Old Crow Loc. 22	25	258.3	80.5	121.2	10	1.6	150.6	
NMC 1552 Old Crow - locality unknown	24	325.0	93.2	137.3	9	1.7	147.3	
NMC 15263 Old Crow Loc. 22	20e	247.4	94.2	98.3+	8.5	1.9	-	
NMC 17659 Whitestone Loc. 43	22	294.8	93.0	95.3+	8	1.8	-	
NMC 9926 Dawson Loc. 12	20e	255.0	96.2	119.8	8	1.9	124.5	
NMC 773 Dawson - locality unknown	22e	322.0	109.1	118.3+	7	1.8	-	
NMC 28957 Johnson Ck.	22	236.4	83.3	131.7	8.5	1.6	158.1	
<i>Mammuthus primigenius</i> .Pleistocene (Maglio 1973, Table 32)								
M	21.8	267.4	87.6	137.8	8.5	1.5	159.7	
OR	20.0- 25.0	207.0- 320.2	65.0- 100.0	123.0- 184.1	6.8- 10.2	1.3- 2.0	137.8- 189.2	
N	5	5	8	8	8	8	8	
SD	1.9	44.1	10.9	20.9	1.1	0.3	10.8	
V	8.8	16.5	12.5	15.2	13.2	18.1	12.4	
M_2 s								
<i>Mammuthus primigenius</i> .Pleistocene, Y.T.								
NMC 26740 Old Crow Loc. 12E	18	176.5	75.0	119.6	10	1.3	159.4	
NMC 20374 Old Crow Loc. 22	17	163.7	64.3	111.0	9.5	1.5	172.6	
<i>Mammuthus primigenius</i> .Pleistocene (Maglio 1973, Table 32)								
M	15.3	174.3	67.0	121.9	9.2	1.3	197.0	
OR	15 - 16	147.0- 185.0	43.0- 85.0	100.0- 136.0	7.6- 11.4	1.0- 2.0	159.8- 232.6	
N	7	5	10	7	9	8	6	
SD	0.5	15.5	12.8	11.4	1.2	0.3	29.8	
V	3.2	8.9	19.1	9.3	13.5	26.0	15.1	

* Measurements follow those of Maglio (1973).

1 - Plate (lamella) number.

2 - Length.

3 - Width.

4 - Height.

5 - Lamellar frequency (number of plate-cement units in a 100 mm interval).

6 - Enamel thickness (average).

7 - Hypsodonty index ($\frac{H}{W} \times 100$).

Table 60. Radiocarbon dates on woolly mammoth (*Mammuthus primigenius*) remains from Siberia (mainly after Heintz and Garutt 1965).

Species	Age (years B.P.)	Laboratory Number	Locality	Remarks
<i>Mammuthus primigenius</i>	29,500 \pm 3000 32,650 \pm 2500 31,500 \pm 2000 44,000 \pm 3500	T-170	Sanga-Yuriak R., Yakutia	Analyses were done on skin and fat from a female mammoth.
"	31,750 \pm 2500 44,000 \pm 3500	T-299	Berezovka R., Yakutia	Analyses of dried blood and fat from a male, the famous Berezovka mammoth.
"	>33,000 35,800 \pm 2700	T-172	Mokhovaya R.	Analyses of skin, fat and sinew.
"	35,800 \pm 1200	T-171	Lena R. delta	Analysis of skin and fat of a male.
"	>30,000	Y-633	Lena R. delta	Analysis of skin from the same specimen at the Radiocarbon laboratory at Yale University.
"	26,000 \pm 1600	MO-215	Lena R.	Analysis of material from a carcass (Kind 1967, p. 182).
"	30,250 \pm 1800 33,500 \pm 1000 33,500 \pm 1000	T-298	Gyda R.	Analysis of skin and fat. The second and third results were given HCl, and HCl and NaOH washes, respectively.
"	11,450 \pm 250	T-297	Mamontova R., Taimyr. Pen.	Analysis of skin, fat and sinew of a male.
"	12,000 (approx.)	-	" "	Analysis of soft parts of the same mammoth in 1954 by A.V. Trofimov of the Geochemical and Analytic-chemical Institute, USSR Academy of Sciences.

will be described elsewhere. It is worth noting that many woolly mammoths seem to have died when they were young, for a few dozen milk molars (not fully worn) have been recovered from ice age deposits in the Yukon.

Referred specimens

NMC 15264 from Old Crow Locality 22 is a complete LM_3 . It has a total of 25 enamel plates, 17 of which were in wear at the time of the animal's death. A piece of mandibular bone is lodged between the two anterior-most roots. The enamel is gray, while the rest of the tooth is brown. NMC 17659 from Whitestone Locality 43 is the nearly complete anterior half of a mandible containing both M_3 s. Nineteen of 22 plates of LM_3 were in wear when the animal died. The enamel is gray, and the rest of the tooth is brown. The specimen was found near the Whitestone mammoth and, like it, may be of mid-Wisconsin age. NMC 9926 from Dawson Locality 12 is an LM_3 . The occlusal margins of the anterior six plates are damaged. Of an estimated 20 plates, 18 were in wear. The enamel is white and the rest of the tooth is light tan. It is probably of late Wisconsin age.

NMC 1552 was collected from an unknown locality on Old Crow River. It is a partly worn (15 of 24 plates

were in wear) RM_3 . The enamel is black, the remainder of the tooth being dark brown. NMC 15263 from Old Crow Locality 22 is an RM_3 with damaged roots. The anterior two plates are heavily eroded. Of an estimated 20 plates, approximately 16 were in wear. The enamel is gray, and the rest of the tooth is dark brown. NMC 773 from an unknown locality in the Dawson Area is an RM_3 . Of an estimated 22 plates, 17 were in wear. The enamel is white, and the rest of the tooth is brown. NMC 28957 from Johnson Creek in the Old Crow Basin is an RM_3 with 22 plates, 14 of which were in wear. Most of the anterior-most plate is missing. The enamel is grayish and the rest of the tooth is brown.

NMC 26470 from Old Crow Locality 12E is a complete LM_2 . Of 18 plates, 11 were in wear when the animal died. The enamel is grayish and the rest of the tooth is brown. NMC 20374 from Old Crow Locality 22 is an RM_2 lacking the anterior roots. Of 17 plates, 15 were in wear. The enamel is gray and the rest of the tooth is stained dark brown.

Discussion

Tooth fragments referable to *Mammuthus* sp. have been found in place in the upper organic subunit of the basal clay, and in the fossiliferous zone (Unit 2) of

Locality 44 in the Old Crow Basin. Therefore, although mammoths are known to have occupied the region from the ?late Illinoian to ?Sangamon time, the exact species is doubtful at present. The darkly stained teeth described here are probably of pre- late Wisconsin age, and NMC 9926 from the Dawson Area is likely to be of late Wisconsin age. In 1975 a fragment of bone from the orbital region of a woolly mammoth was collected in the Sixtymile Area which still has traces of flesh adhering to it. This specimen is of probable late Wisconsin age. Bone from the Whitestone mammoth, which can be readily identified as *Mammuthus primigenius*, gave a radiocarbon date of $30,300 \pm 2,000$ years B.P. (I-3576), indicating presence of woolly mammoths in the northern Yukon during mid-Wisconsin time.

The woolly mammoth has been recorded in several places farther south in Canada. Most of a skeleton was excavated from clay beneath peat near Muirkirk, Ontario (Lambe 1898, p. 137). Organic material with a woolly mammoth tooth buried deeply in gravels near Woodbridge, Ontario yielded a radiocarbon date of $45,000 \pm 900$ years B.P. (GSC-1181), indicating a mid-Wisconsin age for the mammoth (Churcher 1968, p. 219). Leith (1949, p. 137) and Young (1966, p. 96), in reviewing ice age elephant finds in Manitoba, concluded that most represent the

woolly mammoth. There is no information on the age of these fossils.

Important to our understanding of the time of entry of the woolly mammoth into North America are fossils from Medicine Hat, Alberta. There, its remains are identified from sedimentary units considered to be of early Wisconsin and late Wisconsin age (Stalker and Churcher 1970). In British Columbia, woolly mammoth fossils have been identified from the Cariboo and Peace River districts. Radiocarbon analysis of a molar of *M. primigenius* from terrace gravels near Taylor in the Peace River area yielded a date of $27,400 \pm 580$ years B.P. (GSC-2034). Therefore, tundra-adapted mammoths lived in the Peace River region during an interval before ice of the last glaciation covered it. They apparently reoccupied the region after the Wisconsin ice retreated, if a radiocarbon date of $7,670 \pm 170$ years B.P. (I-2244) on a tusk from moraine deposits at Portage Pass is correct (Harrington 1976 MS.).

Remains probably referable to the woolly mammoth have been recorded from various parts of the Northwest Territories including: Tununuk near the mouth of the Mackenzie River, where bone from a specimen

yielded a radiocarbon date of $19,440 \pm 290$ years B.P. (I-8578); the Baillie Islands; and Cape James Ross on Melville Island. The latter specimen is a tusk of an elephant (*Proboscidea* cf. *Mammuthus*), which yielded a radiocarbon date of $21,900 \pm 320$ years B.P. (GSC-1760). It is difficult to explain the presence of mammoths in this part of the Queen Elizabeth Islands during the peak of the Wisconsin glaciation. Perhaps the tusk was rafted along by glacial or sea ice. This is the most northerly mammoth record for North America (Harrington 1976 MS.).

Woolly mammoth remains are occasionally found in the northern part of the conterminous United States, such as in late Wisconsin deposits of the Appalachians (Guilday 1971, p. 252), yet it is often difficult to separate the northern subspecies of the Columbian mammoth (*M. columbi jeffersoni*) from *M. primigenius* because of the similarity of their teeth due to convergent evolution. Aguirre (1969, p. 1376) considers mammoth molars dredged up from the Atlantic continental shelf (Whitmore *et al.* 1967, p. 1477) to lie within the range of *M. columbi columbi* and *M. columbi jeffersoni* (which in thickness of enamel and some other traits, overlaps with *M. primigenius*). He concludes that "a mixed assemblage in the continental shelf is possible."

In Alaska, woolly mammoth fossils have been recorded from many sites such as the arctic coast, St. Lawrence Island, St. Paul Island, Unalaska, Lost Chicken Creek, and particularly the Fairbanks area. Dessicated flesh from a partial carcass found 85 feet (25.9 m) below the surface on Fairbanks Creek, yielded a radiocarbon date of $21,300 \pm 1,300$ years B.P. (L-601), which seems reasonable despite the fact that the specimen was preserved in glycerine. Hair from the skull of a woolly mammoth from Dome Creek gave a date of $32,700 \pm 980$ years B.P. (ST-1632) (Péwé 1975a, p. 99), which is very close to that of the Whitestone mammoth from the Yukon. Although the genus *Mammuthus* is known from Illinoian sediments in central Alaska, there are no definite records of *M. primigenius* in Alaska prior to the Wisconsin glaciation.

Among the Pleistocene vertebrate faunas of northeastern Siberia, an early type of woolly mammoth first occurs in the Utka Beds of the Kolyma Lowland, which appear to be of Riss II (late Illinoian) age (Sher 1971). The species is also known from late Pleistocene (Illinoian to Wisconsin?) deposits on the southern tip of Bolshoi Lyakhov Island in the New Siberian Islands (Vangengeim 1961, p. 55). A late type of the

woolly mammoth is recorded from the early Wisconsin Iedoma Suite and the late Wisconsin Alioshka Suite in the Kolyma Lowland (Sher 1971). Remains have also been found in Wisconsin faunas from Proliv Dmitriya Lapteva and the Berelekh River (Vereshchagin 1974, pp. 3-12). A tusk from the main fossiliferous unit at the latter site yielded a radiocarbon date of $12,240 \pm 160$ years B.P. Other radiocarbon dates on Siberian woolly mammoth remains are provided in Table 60. Apparently this species died out in Siberia between 12,000 and 11,000 years ago.

Woolly mammoths were present in Europe from the Riss II (late Illinoian) to the close of the Würm (Wisconsin) glaciation. Evidently Scandinavia was a refuge for the species during the Eem (Sangamon) interglacial (Heintz 1955, p. 73; 1962, p. 208).

As indicated previously, the woolly mammoth was derived from the steppe mammoth (*M. armeniacus*) in Eurasia toward the end of the Riss II (late Illinoian) glaciation. It appears about the same time in Europe and northeastern Siberia. The earliest forms still resembled their steppe-dwelling ancestors. In later forms a series of progressive changes occurred: molar plates became more numerous and crowded; molar enamel

decreased in thickness; tusk curvature increased; and body size was reduced (Kurtén 1968, pp. 136-137). Such changes provided advantages in masticating the tougher tundra vegetation, and probably the decrease in body size (accompanied by reduction of extremities such as the ears and trunk) and development of a thicker pelt enabled them to survive under increasingly cold conditions.

The late form of *M. primigenius* first appeared in the early part of the Würm (Wisconsin) glaciation in Siberia. Evidence from Medicine Hat, Alberta suggests that the woolly mammoth first reached North America from Siberia via the Bering Isthmus during the early Wisconsin, although a late Illinoian crossing is still possible. The critical evidence on this matter probably still lies in the ground in Alaska and the Yukon Territory. The species spread rapidly during the mid-Wisconsin reaching eastern Canada about 45,000 years ago, and evidently becoming extinct in North America some 8,000 years ago.

Woolly mammoths were Holarctic in their distribution probably, originating in and spreading from north central Eurasia westward to England and Spain, and eastward to the tundra or tundra-like regions of northern North America including the Appalachians and

the Atlantic coastal region of the northern United States (Hay 1923b, pp. 131-132). The species was common in Eastern Beringia during the last glaciation.

A great deal is known about the appearance of this species as a result of the discovery of some well preserved carcasses from the permafrost of Siberia, and from many detailed carvings, engravings and murals in caves by Paleolithic artists in southwestern Europe. These mammoths were about 3 m high at the shoulders – smaller than most late Pleistocene members of the genus, and about the size of modern Asiatic elephants. Perhaps their most remarkable features were: the long, hanging hair consisting of coarse, dark reddish, brown guard hairs and fine, muskox-like underwool (Ryder 1974, p. 190); large elaborately curved tusks; a high, peaked head which appears knob-like in many cave depictions; a high hump resulting from the long spines of the cervical vertebrae, possibly accentuated by fat deposits and thick hair; a steeply sloping back; relatively small ears; and a trunk shorter than those of living elephants (Kurtén 1968, pp. 137-138).

The habitat of the woolly mammoth is clearly indicated by its physical appearance and food habits.

All evidence points to its adaptation to cold climatic conditions, and generally, it can be considered as a reliable paleoenvironmental indicator of tundra, tundra-boreal forest margin, or cold loess-steppe.

Stomach contents found with frozen carcasses reveal an abundance of grasses, sedges and other boreal meadow and tundra plants, along with a few twigs, conifer cones, and pollen of high-boreal and tundra trees. Sixty species of plants have been determined from the stomach contents of the well known Berezovka mammoth – one of the best preserved woolly mammoths (Farrand 1961, Table 1). Food in the stomach of this mammoth weighed about 33 pounds (15 kg) (Augusta and Burian 1962, p. 18). I think it possible that woolly mammoths could have been migratory to some extent, feeding on grasses, sedges and willows of the tundra during the summer and autumn, and moving toward the tree-line in winter, where heavy shrubs and stunted trees may have provided fodder. The question is debatable.

How the species adapted to water shortage in winter is unknown. To conserve water physiologically during winter conditions, it would seem reasonable that their winter droppings would have been dry – perhaps

like muskox, moose or caribou pellets, only larger. Yet, to my knowledge no recognizable fossil droppings have been reported. Did they break ice on ponds or streams to get at water, or did they obtain sufficient liquid by taking in snow with their normal food? Many fundamental questions concerning the survival of large elephants in the arctic have yet to be answered.

Scimitar cats may have preyed on the young, but the adults would have been formidable adversaries. There is increasing evidence that Paleolithic hunters killed woolly mammoths in great numbers in Eurasia, particularly in the Ukraine, where the species was of basic economic importance (Pidoplichko 1969; Klein 1973). In the Old Crow Basin of the Yukon, mammoth limb bones often show signs of breakage by man. Special techniques were probably developed there for making and using mammoth bone tools (Harington *et al.* 1975, p. 47). In Alaska, two fluted points were found *in situ* 60 feet (18.2 m) from the surface in frozen muck. One of them was directly associated with bones of a young "mastodon" {presumably a woolly mammoth - CRH} (Rainey 1940).

Order Perissodactyla

Family Equidae

Equus cf. (*Plesippus*) *verae* (large horse)

Remains of horses are the most common vertebrate fossils recovered from the Yukon Pleistocene deposits. Several thousand specimens (mainly teeth, metapodials, carpals, tarsals and phalanges) from Dawson, Old Crow and other areas are in the Quaternary Zoology collection.

E. Ann Holland of the University of Toronto began a statistical study of the horse specimens in this collection in 1973. Pending the results of her more detailed study, I will summarize my views of the kinds of horses that occupied the Yukon Territory during the Pleistocene mainly by reference to a series of complete metapodials. Generally speaking, metapodial length is related to length of stride and speed, while metapodial stoutness varies directly with the size and weight of the horse. The possible phylogenetic value of horse metapodials has been mentioned by Forsten (1973, p. 3), and a few detailed metric studies have been carried out on late Cenozoic horses (e.g. Willoughby 1948, Howe 1969). Scattergrams relating total length to proximal width of metapodials seem to offer a useful method of separating various species of horses, zebras

and wild asses, and this method (Lundelius and Stevens 1970, Figure 3; Harington and Clulow 1973, Figure 28) is applied here to complete Pleistocene horse metapodials from the Yukon in an attempt to indicate the various kinds of horses represented in collections from that region (Figure 60A-B).

Fossils of large horses (Figures 58A-B, 59A-D, 60A-B, 62B-D, Tables 61-62) are most commonly found in the Old Crow Basin of the Yukon. Unfortunately no significant cranial or mandibular specimens with teeth have been recovered yet, although many separate teeth belonging to this species have been collected. Generally, the molars are large, and the upper molars are often characterized by complex enamel folding (particularly on the posterior margin of the prefossette and the anterior margin of the postfossette). The complexity of the enamel is not entirely a function of age, for well-worn teeth often show this feature (e.g. NMC 20830 and 19034 from Old Crow Localities 29 and 66 respectively; Figure 62B-C). Also, hypostylar fossettes (see Quinn 1955, Figure 1) are commonly seen (e.g. NMC 20830; Figure 62C) in upper molars of the large horses of the Yukon Pleistocene. Similar features are noted in *Equus (Plesippus) idahoensis* of the late Pliocene

Figure 58. Comparisons of metapodials of large horses from the Pleistocene of the Yukon Territory.

A. Posterior views (from left to right): right metatarsal lacking the distal end (NMC 16524, Old Crow Locality 12) of a Pleistocene giant horse (*Equus* sp.); right metatarsal (NMC 15080, Old Crow Locality 69) of a Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*); right metacarpal (NMC 16324, Old Crow Locality 65) of a Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*); right metacarpal (NMC 13660, Old Crow Locality 11A) of a Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*). B. Anterior views (from left to right): NMC 16524; NMC 15080; NMC 16324; NMC 13660.

A

5 CM

B





Figure 1. A schematic diagram of the experimental setup. The diagram shows a subject sitting at a table, looking at a screen. The screen displays a visual stimulus. The subject's response is recorded by a computer. The diagram is labeled with 'Subject', 'Screen', 'Stimulus', and 'Computer'.

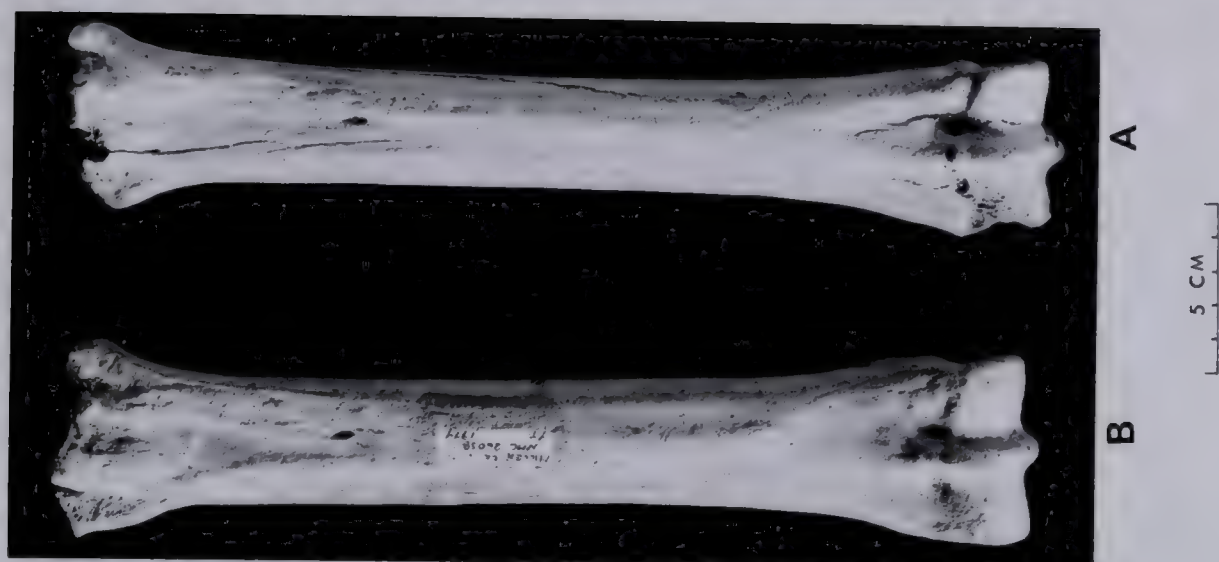


Figure 59. A. Posterior view of a right metatarsal (NMC 25265, Sixtymile Locality 2) of a Pleistocene large horse (*Equus* cf. *Plesippus* *verae*).

B. Posterior view of a right metatarsal (NMC 26038, Sixtymile Locality 2) of a Pleistocene large horse (*Equus* cf. *Plesippus* *verae*). Note the light color of these metatarsals compared to the darkly stained metapodials from the Old Crow Basin (Figure 58).

C. Dorsal view of a third phalanx (NMC 13655, Old Crow Locality 11A) of a Pleistocene large horse (*Equus* cf. *Plesippus* *verae*).

D. Ventral view of NMC 13655. Note the large size of this hoof.



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D



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Figure 60. A. Scattergram of total length in relation to proximal width of Yukon Pleistocene horse metacarpals referred to: A. Yukon wild ass (*Equus (Asinus) lambei*); B. large horse (*Equus* cf. (*Plesippus*) *verae*); C. medium-sized horse (*Equus* cf. *scotti*).

B. Scattergram of total length in relation to proximal width of Yukon Pleistocene horse metatarsals referred to: A. Yukon wild ass (*Equus (Asinus) lambei*); B. large horse (*Equus* cf. (*Plesippus*) *verae*); C. medium-sized horse (*Equus* cf. *scotti*); D. kiang-like wild ass (*Equus (Asinus)* cf. *kiang*); E. giant horse (*Equus* sp.).

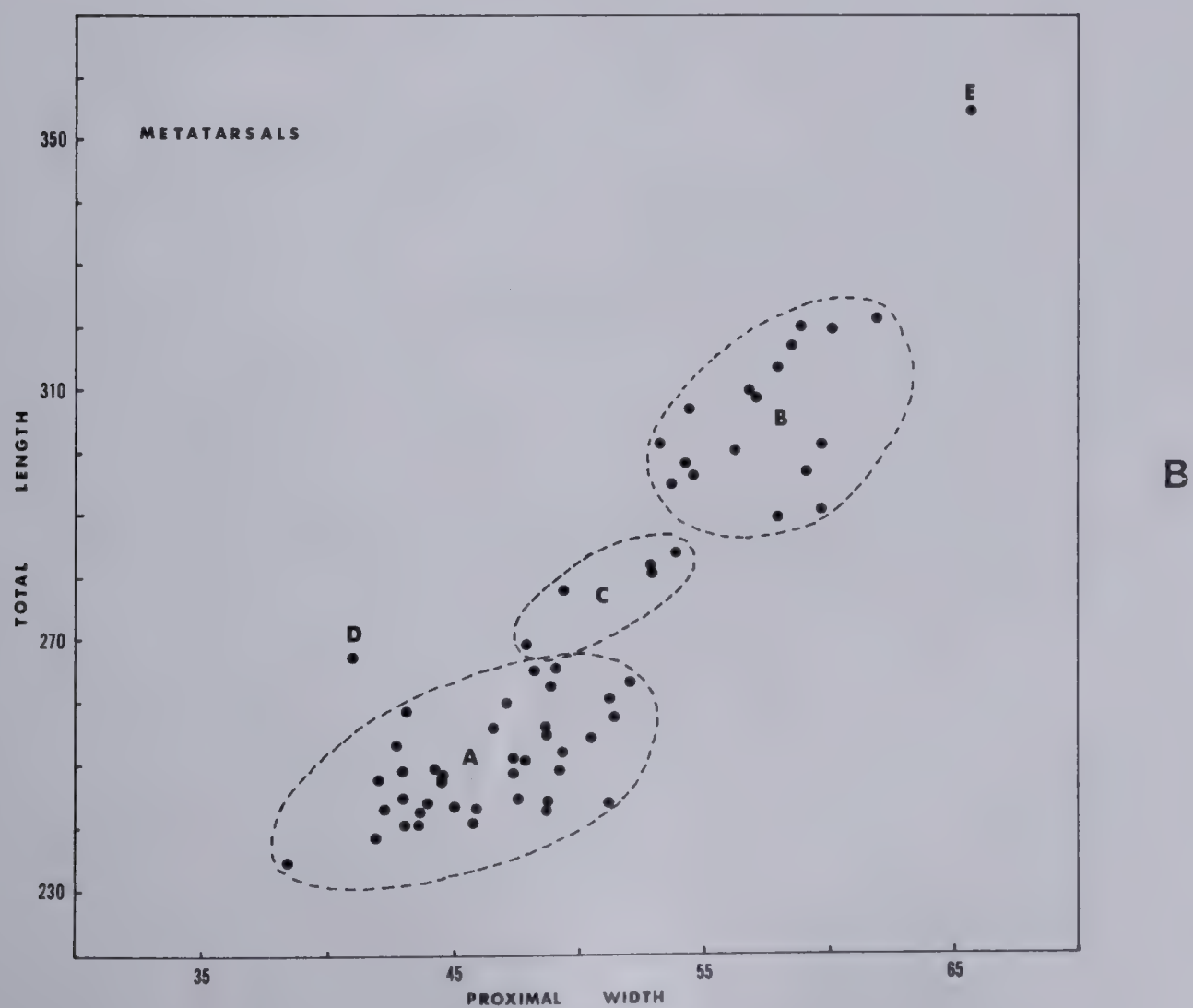
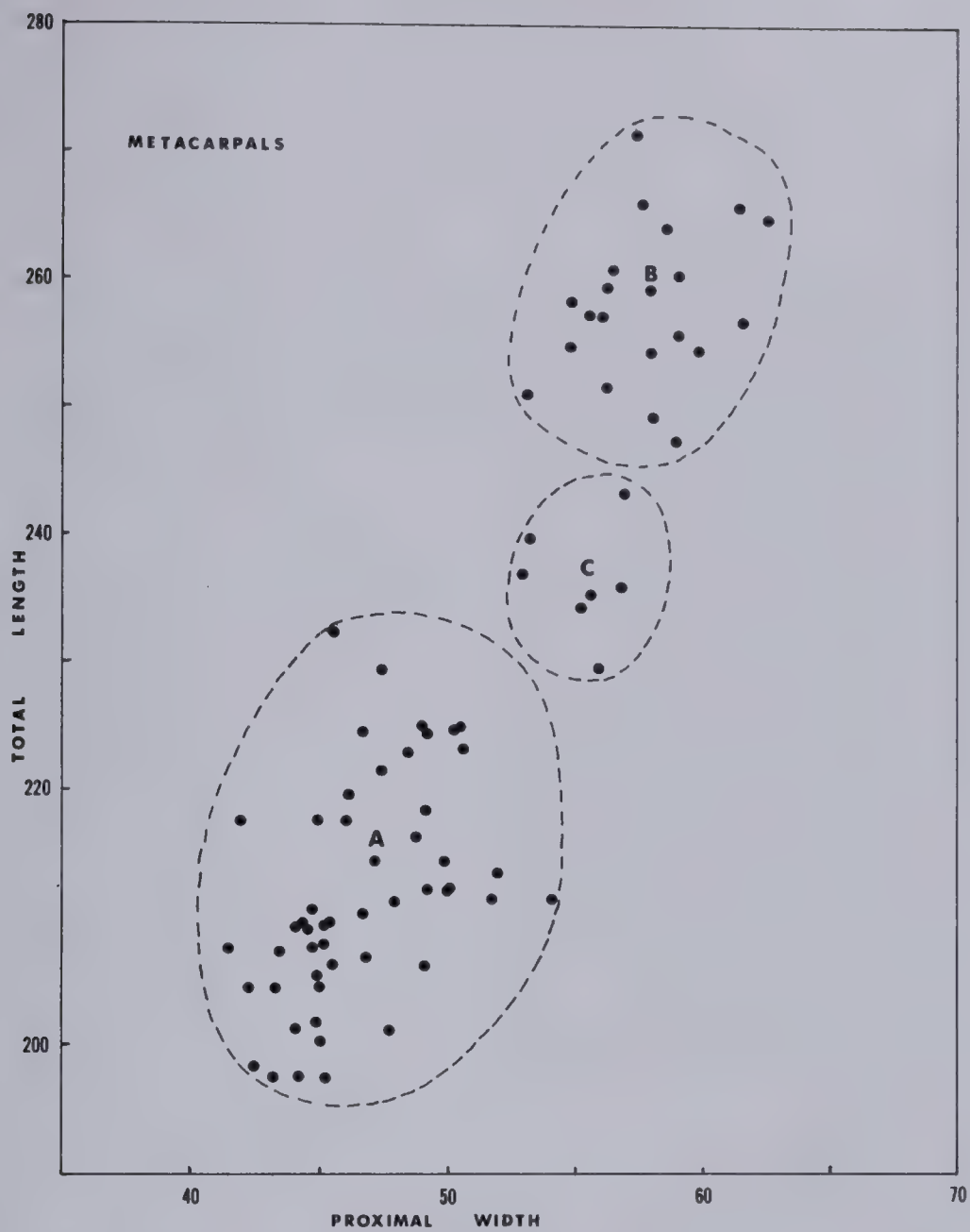


Table 61. Measurements of Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*) metacarpals from the Yukon Territory compared to those of Pleistocene *E. (P.) verae* from Siberia and Pliocene *E. (P.) idahoensis* from the United States.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Equus</i> cf. (<i>Plesippus</i>) <i>verae</i> , Pleistocene, Y.T.							
NMC 19910 Old Crow Loc. 29	271.5	57.3	38.4	39.4	31.6	53.0	43.8
NMC 19324 Old Crow Loc. 65	266.0	57.6	38.5	40.4	28.2	57.2	45.8
NMC 23293 Old Crow Loc. 84	265.8	61.4	42.2	40.6	29.6	56.2	44.8
NMC 13660 Old Crow Loc. 11A	264.9	62.5	41.1	44.5	30.3	58.2	43.2
NMC 18192 Old Crow Loc. 29	264.1	58.5	39.0	39.0	30.1	53.1	42.2
NMC 14355 Old Crow Loc. 15	260.9	56.4	40.0e	39.0	32.0e	-	43.7
NMC 20493 Old Crow Loc. 20	260.3	57.9	38.4	38.1	28.2	56.2	42.5
NMC 28298 Old Crow Loc. 136	259.5	56.2	37.5	40.2	32.2	52.9	42.0
NMC 16905 Old Crow Loc. 42	259.3	57.9	37.8	40.3	29.9	53.9	42.6
NMC 20759 Old Crow Loc. 29	258.3	54.7	37.0	38.5	28.1	50.0	41.8
NMC 23368 Old Crow Loc. 42	257.2	55.5	35.8	38.5	28.3	55.5	39.7
NMC 14658 Old Crow Loc. 25	257.1	56.0	37.0	37.7	27.5	55.5	39.9
NMC 26633 Old Crow Loc. 11	256.9	63.9e	37.5	42.3	30.9	57.3	-
NMC 20555 Old Crow Loc. 32E	255.8	59.0	39.0	38.0	29.0	58.0	40.5
NMC 20617 Old Crow Loc. 22	254.9	54.7	38.2	37.6	28.2	53.7	43.3
NMC 27393 Old Crow Loc. 60	254.5	59.8	40.6	38.4	28.0	57.0	41.1
NMC 20760 Old Crow Loc. 29	254.3	57.5	38.5	38.3	27.1	54.7	41.2
NMC 16732 Old Crow Loc. 14N	253.7	56.2	38.2	39.2	29.2	51.6	42.0
NMC 14186 Old Crow Loc. 12	251.0	52.0	36.9	37.4	28.3	51.7	40.0
NMC 20627 Old Crow Loc. 22	249.1	58.0	37.6	40.3	28.7	55.0	42.2
NMC 20092 Old Crow Loc. 74	247.4	58.9	37.2	38.9	30.9	56.1	44.0
<i>Equus (Plesippus) verae</i> , Pleistocene, Siberia**							
PIN 2998 74	267.1	60.6	38.6	40.8	29.6	56.1	41.2
PIN uncataloged	261.8	66.7	41.2	43.9	30.6	62.7	43.4
PIN <u>835-243</u> 27	260.2	63.9	41.5	43.6	30.4	60.1	44.6
PIN 2998-27	259.3	59.9	39.7	40.7	27.4	56.9	41.2
PIN <u>835-529</u> 32	256.7	58.3	39.5	39.2	30.4	56.5	39.3
<i>Equus (Plesippus) idahoensis</i> , late Pliocene, Idaho (Shotwell 1970, Table 22)							
M	205.0	57.0	35.0	-	-	-	-
OR	225.0- 280.0	48.0- 66.0	32.0- 39.0	-	-	-	-
N	9	9	9	-	-	-	-

- * 1 - Total length.
 2 - Proximal width.
 3 - Proximal depth.
 4 - Midshaft width.
 5 - Midshaft depth.
 6 - Distal width.
 7 - Distal depth.

** A.V. Sher kindly allowed me to take these measurements from specimens collected by him and preserved in the Paleontological Institute, Academy of Sciences of the USSR, Moscow.

Table 62. Measurements of Pleistocene large and giant horse (*Equus* cf. (*Plesippus*) *verae* and *Equus* sp.) metatarsals from the Yukon Territory compared to those of Pleistocene *E. (P.) verae* from Siberia and late Pliocene *E. (P.) idahoensis* from the United States.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Equus</i> sp. Pleistocene, Y.T.							
NMC 16524 Old Crow Loc. 12	354.2e	65.6	52.8	43.0	37.5	-	-
<i>Equus</i> cf. (<i>Plesippus</i>) <i>verae</i> . Pleistocene, Y.T.							
NMC 21029 Old Crow Loc. 14	321.0	61.8	47.7	41.0	33.8	59.3	44.7
NMC 22939 Old Crow Loc. 12	320.0	58.8	49.3	38.8	33.5	58.9	44.1
NMC 17295 Dawson Loc. 28	319.6	60.1	47.5	37.4	34.2	56.8	44.9
NMC 14486 Old Crow Loc. 22	316.7	58.4	48.0	38.8	32.6	56.5	41.4
NMC 24025 Old Crow Loc. 20	313.4	57.9	48.2	37.5	32.2	55.8	42.9
NMC 27366 Old Crow Loc. 45	309.8	56.7	46.0	37.4	32.0	55.5	41.9
NMC 15080 Old Crow Loc. 69	308.3	57.0	46.9	38.6	34.7	56.9	42.9
NMC 29039 Dawson Loc. 10	306.5	54.4	45.9	27.0	35.8	50.2	41.9
NMC 20616 Old Crow Loc. 22	301.3	53.2	44.8	31.2	30.1	52.6	42.7
NMC 27365 Old Crow Loc. 45	300.8	59.7	50.3	36.5	36.7	57.0	42.5*
NMC 27912 Old Crow Loc. 71	300.0	56.1	48.6	38.1	36.0	54.2	42.6
NMC 25265 Sixtymile Loc. 2	298.0e	54.1e	46.4	33.5	35.2	50.3	43.5
NMC 15334 Old Crow Loc. 22	296.4	59.0	47.7	40.3	35.0	58.7	45.5
NMC 27886 Old Crow Loc. 87	296.0	54.5	45.1	34.4	33.6	50.4	41.6
NMC 18980 Old Crow Loc. 29	294.2	53.6	46.0	37.8	35.3	54.9	42.4
NMC 26887 Old Crow Loc. 22	290.4	59.7	46.9	37.4	35.8	56.9	44.0
NMC 26038 Sixtymile Loc. 2	289.6	57.9	46.8	36.4	34.4	54.7	41.2
<i>Equus (Plesippus) verae</i> . Pleistocene, Siberia**							
PIN $\frac{835-552}{34}$	326.0	61.8	52.0	39.8	35.8	58.9	45.0
PIN 2998-131	323.0	61.2	49.9	40.4	34.3	59.7	44.4
PIN 2998-34	313.7	61.9	51.4e	40.4	35.6	58.8	44.2
PIN uncataloged	313.4	60.0	50.2	40.7	36.2	60.0	44.5
PIN $\frac{825-234}{27}$	306.4	53.1	44.8	33.5	29.0	54.1	41.2
<i>Equus (Plesippus) idahoensis</i> . late Pliocene, Idaho (Shotwell 1970, Table 22)							
M	300.0	56.0	47.0	-	-	-	-
OR	298.0- 315.0	53.0- 59.0	45.0- 51.0	-	-	-	-
N	5	5	5	-	-	-	-

- * 1 - Total length.
 2 - Proximal width.
 3 - Proximal depth.
 4 - Midshaft width.
 5 - Midshaft depth.
 6 - Distal width.
 7 - Distal depth.

** A.V. Sher kindly allowed me to take these measurements from specimens collected by him and preserved in the Paleontological Institute, Academy of Sciences of the USSR, Moscow.

Grand View fauna of Idaho, and lower premolars such as P_4 (NMC 26049; Figure 62D) are closely matched in size and enamel pattern by specimens of *E. (P.) idahoensis* (Shotwell 1970, Figure 41 L,C).

In 1973, during a visit to several Soviet museums, sponsored by the Paleontological Institute of the Academy of Sciences of the USSR, I was able to compare lower forelimb and hindlimb bones of the large horse from the Old Crow Basin directly with similar elements of *Equus (Plesippus) verae* collected by A.V. Sher from the Olyor Suite (Mindel = ?Kansan) in the Kolyma Lowland of northeastern Siberia. They were almost exactly the same - even to their blackish brown staining. An upper molar with its characteristic complex enamel pattern was readily matched by specimens of *E. (P.) verae* in Sher's collection. Therefore, except for NMC 16524, the largest metapodials are referred to a large horse like *Equus (Plesippus) verae*. Further comparisons are required with some of the large North American Pleistocene horses such as *Equus (Plesippus) idahoensis* and *Equus (?Plesippus) giganteus*.

Referred specimens

The following metacarpals (III) are referred:
right - NMC 16324 (Old Crow Locality 65), 13660 (Old Crow Locality 11A), 14355 (Old Crow Locality 15),

28292 (Old Crow Locality 136), 26633 (Old Crow Locality 11), 16732 (Old Crow Locality 14N), 20493 (Old Crow Locality 20), 23368 (Old Crow Locality 42), 20555 (Old Crow Locality 32E), 16905 (Old Crow Locality 42), 14658 (Old Crow Locality 25), 20092 (Old Crow Locality 74); left - NMC 27393 (Old Crow Locality 60), 14186 (Old Crow Locality 12), 23293 (Old Crow Locality 84), 20627, 20617 (Old Crow Locality 22), 20759, 18910, 20760, 18102 (Old Crow Locality 29).

These specimens are stained brown to blackish brown.

NMC 13660 appears to represent an old individual according to development of a ridge of callus along the medial margin where metacarpal II was strongly fused to metacarpal III (see Harington and Clulow 1973, p. 721) - a view supported by the large size of the latter bone. Similarly, NMC 16732 may be old because metacarpal IV is fused to metacarpal III. Exostoses at the proximal end of NMC 23293 are also suggestive evidence that an old individual is represented. NMC 14355 is interesting because of an exostoseal lesion above its distal articulation. NMC 20627 has a "fresh" impact mark 17 mm above the anterior surface of the distal articulation, which seems to have been made about the time of the death of the animal. In part, it may have had to do with the death of the horse. It could be the result of a human blow, or possibly a compression mark made by crushing teeth of a large

carnivore. The latter suggestion seems unlikely because no tooth marks are visible on the posterior surface of the bone at the same general level. Could the healing of a similar blow or bite have resulted in the pathological proliferation of bone in the same place on NMC 14355? NMC 20760 has a 10 mm x 9 mm facet on the medial side of the distal articular surface. Parallel striae and dark staining on this facet suggest a saw-like cut may have been made there on fresh bone - possibly by people in the process of butchering the animal. Most metacarpals have total lengths lying between 247 and 272 mm.

The following metatarsals are referred: right - NMC 16524 (Old Crow Locality 12), 21029 (Old Crow Locality 14), 22939 (Old Crow Locality 12), 24025 (Old Crow Locality 20), 15080 (Old Crow Locality 69), 20616 (Old Crow Locality 22), 27365 (Old Crow Locality 45); left - NMC 17295 (Dawson Locality 28), 14486 (Old Crow Locality 22), 27366 (Old Crow Locality 45), 29039 (Dawson Locality 10), 27912 (Old Crow Locality 71), 25265 (Sixtymile Locality 2), 15334 (Old Crow Locality 22), 27886 (Old Crow Locality 87), 18980 (Old Crow Locality 29), 26038 (Sixtymile Locality 2), 26887 (Old Crow Locality 22). All of these specimens are stained dark brown except

NMC 29039 from Hunker Creek, which is light buff and NMC 25265 from Miller Creek, which is tan. Both show grooves of rootlets on their surface, possibly indicating death in a grassland environment. NMC 20616 is very slender compared to the other metatarsals. Most metatarsals range in total length from 288 to 322 mm, averaging somewhat less than four specimens of *E. (P.) verae* (Sher 1971, Table 20).

Measurements of the Yukon metacarpals and metatarsals lie within the general size range of *E. (P.) verae* of northeastern Siberia and *E. (P.) idahoensis* of southern North America (Tables 61-62).

Discussion

Teeth and other elements tentatively referred to this large horse have been excavated *in situ* from the upper organic subunit of the basal clay at Old Crow Localities 11 and 12, and from Unit 2 at Old Crow Locality 44; thus, the species may have lived in the Old Crow Basin from late Illinoian to Sangamon time. The fresh appearance of NMC 29039 from the Dawson Area suggests that the species may have survived until late Wisconsin time there. I know of no other fossils from Canada that can be referred with confidence to this species, although "*Equus* cf. *giganteus*" from

mid-Wisconsin sediments at Medicine Hat, Alberta (Stalker and Churcher 1970) is possibly related.

A fundamental problem in making valid comparisons is the lack of a critical, wide-ranging statistical review of North American Pleistocene horses, although Savage (1951, pp. 243-353) has made an admirable attempt to clarify the problem. Scores of species have been named, many based on poor and fragmentary holotypes.

Large horses are rarely mentioned from Pleistocene deposits in Alaska. A third phalanx of "*Equus* sp." from ?Nebraskan sediments at Cape Deceit may belong to an ancestor of *E. (P.) verae* (Harrington 1976 MS. p. 87). Guthrie and Matthews (1971, p. 495) note that it "is larger than most of those that were collected from deposits of Illinoian and Wisconsin age in the Fairbanks area of interior Alaska".

In northeastern Siberia, large horses of this general type are first represented by "*Equus (Plesippus)* sp." in the early Pleistocene (?Nebraskan) Begunov Suite (Sher 1971), and they may have lived at approximately the same time in western Alaska (Cape Deceit). *E. (P.) verae* first appeared in Siberia about Mindel (?Kansan) time,

being the dominant horse then, and later giving way to a large form of *Equus caballus*. Sher (1971) feels that the former species is more closely related to *E. süssenbornensis* of Europe than to coeval central Asian horses of the *sanmeniensis-sivalensis* type. The zebrine horses of Europe, including *E. süssenbornensis* and its possible predecessor *E. stenonis*, lived from the mid-Villafranchian to the Günz II (?late Nebraskan) glacial (Kurtén 1968, pp. 148-149). Referring to *E. (P.) verae*, Sher (1971, p. 152) states, "So far horses of such type are unknown in America, but theoretically it can be supposed that they will be encountered among the later forms of *Plesippus*." Evidence presented here suggests that this kind of horse was present in the Yukon from at least ?late Illinoian to possibly late Wisconsin time. Like *Alces latifrons*, this species seems to have survived in Eastern Beringia long after its extinction elsewhere.

Compared to later evolving caballine horses, this species was large, reaching an estimated 1.7 m at the shoulder. It had relatively long, slender legs and large hooves (Figure 59C-D). Sher (1971, p. 152) suggests that *E. (P.) verae* was adapted to swift movement over open, fairly solid plains (perhaps not so solid as in

contemporaneous steppe regions of southern Europe which were occupied by related horses). Rootlet impressions on the surface of some of the metapodials from the Yukon may imply that the horses they represent died in grassland surroundings. I speculate that the unusually large size of this horse, its correspondingly large cheek teeth, and above all, the extraordinary complexity of enamel patterns on their teeth, are indicative of a form rapidly exploiting a fresh environmental niche, consisting of broad plains with relatively tough grassy forage. Why it gave way to smaller, simpler-toothed caballine horses is an interesting question, for the complexity of the molars of woolly mammoths (*Mammuthus primigenius*) apparently better enabled them to survive in large numbers throughout Eurasia until the close of the last glaciation. The large Yukon horses occasionally had pathological problems as indicated by the occurrence of an exostoseal lesion just above the distal articulation of a metacarpal (NMC 14355) from the Old Crow Basin (Choquette *et al.* 1975, p. 1055). In the Yukon Territory, presumably large cats such as the American lion (*Panthera leo atrox*) and perhaps the American scimitar cat (*Homotherium serum*) were their main predators. Wolves may have preyed on these horses occasionally. Likely, people also hunted them, for bones

of large Pleistocene horses often show signs of breakage by man (Harington *et al.* 1975, p. 46). Considering the length of their legs and the size of their hooves, mature horses were probably formidable opponents.

Equus sp. (giant horse)

Referred specimen

A single right metatarsal, NMC 16524 from Old Crow Locality 12 (Figure 58A-B, 60B, Table 62), is much larger than any other horse metatarsals recovered from Pleistocene deposits of the Yukon. Although the distal articulation has been broken away leaving a specimen 320.3 mm long, it is not difficult to estimate by means of ratios the length of the missing portion. I consider the total length of this metatarsal to have been approximately 354 mm. That is about 33 mm more than the longest metatarsal in the collection referred to *Equus* cf. (*Plesippus*) *verae* from the Yukon Territory, and 28 mm more than the longest metatarsal of *E. (P.) verae* from Siberia that I was able to measure (Table 62). The fossil is dark brown on the posterior surface and light brown elsewhere. I can see no qualitative features by which it can be differentiated from the other large horse fossils.

Discussion

Perhaps NMC 16524 represents an unusually large ancestor of *Equus* cf. (*Plesippus*) *verae*.

Equus cf. *scotti* (medium-sized horse)

Seven metacarpals and five metatarsals (Table 63) represent a horse intermediate in size between the relatively small Yukon wild ass (*Equus* (*Asinus*) *lambei*) and the large horse (*Equus* cf. (*Plesippus*) *verae*). Among Pleistocene horse metapodials with which I am familiar, these specimens best match those of *Equus scotti*, and they are referred to a horse of that kind. Pending further evidence, I follow Savage (1951, p. 251) in considering *Equus niobrarensis* and *Equus hatcheri* as junior synonyms of *Equus scotti*.

Referred specimens

Seven metacarpals are referred to *Equus* cf. *scotti*: right - NMC 13658 (Old Crow Locality 11A), 26850 (Old Crow Locality 22), 29038 (Dawson Locality 10); left - NMC 28126 (Old Crow Locality 126), 26686 (Old Crow Locality 20), 22861 (Old Crow Locality 22), 14485 (Old Crow Locality 22). All are stained dark brown but the Dawson Area specimen NMC 29038, which is pale tan and has pyrolusite "stars" on its surface. This specimen and NMC 13658 appear to represent relatively old individuals, for in the former, metacarpal IV is fused

Table 63. . Measurements of Pleistocene medium-sized horse (*Equus* cf. *scottii*) metapodials from the Yukon Territory compared to those of Pleistocene *E. scottii* from Texas and Saskatchewan.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
Metacarpals							
<i>Equus</i> cf. <i>scottii</i> . Pleistocene, Y.T.							
NMC 26686 Old Crow Loc. 20	243.3	56.8	39.9	39.1	30.0	56.0	41.6
NMC 26850 Old Crow Loc. 22	239.9	53.1	34.5	32.3	24.6	49.5	37.0
NMC 29038 Dawson Loc. 10	238.2	53.0	36.2	34.4	27.2	49.1	38.5
NMC 28126 Old Crow Loc. 126	236.0	55.9	38.0	34.2e	27.3	48.3	40.6
NMC 22861 Old Crow Loc. 22	235.9	56.7	38.8	40.0	30.0	52.3	39.8 ⁺
NMC 14485 Old Crow Loc. 22	234.4	55.1	36.5	35.1	25.7	54.2	41.3
NMC 13658 Old Crow Loc. 11A	229.6	55.9	38.7	38.7	26.6	53.1	37.1
<i>Equus scottii</i> . Pleistocene, Texas,							
Rock Creek (Troxell 1915, p. 620)	244.0	57.3	41.5	41.0	-	57.7	42.7
<i>Equus scottii</i> . Pleistocene, Saskatchewan							
SM-156 Saskatoon Site, Saskatoon	250.5	52.6	38.1	38.5	29.9	48.3	38.4
NMC 26097 Saskatoon Site, Saskatoon	248.0	53.6	38.6	37.9	31.2	50.8 ⁺	43.0e
Metatarsals							
<i>Equus</i> cf. <i>scottii</i> . Pleistocene, Y.T.							
NMC 17573 Dawson Loc. 30	283.9	53.9	44.6	35.9	36.7	50.7	38.1
NMC 17293 Dawson Loc. 7	281.6	53.0	44.5	34.1	32.9	51.2	41.0
NMC 28964 Dawson Loc. 17	280.3	52.9	44.0	33.1	30.7	51.7	40.0
NMC 29067 Sixtymile Loc. 3	277.6	49.3	39.9	29.1	31.2	47.3	36.8
NMC 23392 Old Crow Loc. 11A	269.2	47.8	40.6	32.3	31.2	44.4	35.8
<i>Equus scottii</i> . Pleistocene, Texas							
NMC 2381 Rock Creek	277.0e	56.7	49.2	37.9	38.1	53.9	39.5e
<i>Equus scottii</i> . Pleistocene, Saskatchewan							
SM-152 Saskatoon Site, Saskatchewan	299.2	50.2	44.4	34.0	33.9	50.3	38.9
NMC 11869 Fort Qu'Appelle	291.7	47.6	42.0	34.6	34.5	46.9	37.5
NMC 12218 Fort Qu'Appelle	289.2	49.8	43.4	34.0	32.8	48.0	38.1
SM-4 Saskatoon Site	284.3	48.5	40.6	33.7	30.8	-	36.2
NMC 12219 Fort Qu'Appelle	275.0	48.1	42.2	31.8	32.2	46.5	37.1
NMC 12144 Fort Qu'Appelle	268.3	43.4	38.3	36.8	30.3	42.4 ⁺	-
NMC 11902 Fort Qu'Appelle	266.2	42.9	40.9	31.3	33.4	40.9 ⁺	35.2

- * 1 - Total length.
 2 - Proximal width.
 3 - Proximal depth.
 4 - Midshaft width.
 5 - Midshaft depth.
 6 - Distal width.
 7 - Distal depth.

strongly to metacarpal III, and in the latter, bony proliferation indicates that metacarpal II was strongly fused to metacarpal III. NMC 26850 seems to represent a horse in very early maturity or late immaturity for the distal epiphyseal suture is still visible. NMC 14485 has a network of rootlet impressions on its dorsal surface. These metacarpals lie between the series of small Yukon wild ass metacarpals, and that of large horse metacarpals. NMC 26686 matches very closely a metacarpal of *E. scotti* from Rock Creek, Texas, the type locality of this species (Gidley 1900). Specimens of *E. scotti* from Sangamon interglacial or mid-Wisconsin deposits at Saskatoon, Saskatchewan are slightly larger in size than most of the Yukon fossils.

The following metatarsals are referred: right - NMC 28964 (Dawson Locality 17), 29067 (Sixtymile Locality 3); left - NMC 17573 (Dawson Locality 30), 17293 (Dawson Locality 7), 23392 (Old Crow Locality 11A). The last specimen from the Old Crow Area is stained blackish brown like the metacarpal NMC 26686. The remaining specimens from the Dawson and Sixtymile areas are paler - particularly NMC 29067, which appears to be of late Wisconsin age. NMC 17573 is unusual in that it is grayish. It has rootlet impressions on its surface. Probably larger samples of *Equus* cf. *scotti* metapodials would result in their overlapping the size ranges of both the Yukon wild ass and large horse metapodials.

Discussion

This appears to be the first report of a horse like *E. scotti* from Eastern Beringia. The darkly stained specimens from the Old Crow Basin suggest that these medium-sized horses arrived there from the southern plains of North America before the late Wisconsin. The species seems to have been commoner farther south (in the Dawson - Sixtymile region), probably during the late Wisconsin.

Hay (1913b) described a complete horse skull from the Tofty mining district of Alaska under the name *Equus niobrarensis alaskae*. I doubt that this specimen represents *E. niobrarensis* (= *E. scotti*). Comparison of good casts of the entire upper dentitions of the types of *Equus niobrarensis alaskae* (USNM 7700) and *Equus (Asinus) lambei* (USNM 8426) with a complete cranium of *E. scotti* (NMC 2381) from the type locality of that species suggests to me that:

(a) USNM 7700 and 8426 are basically similar in conformation, having similar P^2-M^3 alveolar lengths, simple enamel patterns on the occlusal surfaces of the cheek teeth, and facial crests lying relatively close to the alveolar margin of the upper cheek teeth; (b) the approximately 8 mm longer diastema length and greater breadth across I^3 s of USNM 7700 relative to USNM 8426 are probably functions of differences in sex and age; the former represents an approximately

6-year-old male (well developed canines and slightly worn incisors), while the latter evidently represents an old female (no canines or canine swellings and heavily worn incisors). Furthermore, USNM 7700 is closely matched by a good cranium of what I consider to be a male *E. (A.) lambei* (NMC 9924) from Hunker Creek in the Dawson Area. It is also interesting to note that Repenning *et al.* (1964, Table 1) have identified remains of a species of small horse rather than a medium-sized horse from Pleistocene deposits in the Tofty mining district – the type locality of *E. niobrarensis alaskae*;

(c) USNM 7700 is notably smaller than a similar-aged female (lacking canines with slightly worn incisors) of *E. scotti* (NMC 2381). In alveolar length alone the former is approximately 13% smaller than the latter. The distance from the facial crest to the alveolar margin of the upper cheek teeth is much greater in NMC 2381 than in either USNM 7700 or 8426. Therefore, it appears that medium-sized horses like *E. scotti* have not yet been reported from Alaska, although there is every reason to suspect that they lived there during the late Pleistocene.

In southern Canada, *E. scotti* first appears in deposits of Kansan age at Medicine Hat, Alberta. It is recorded there also in faunas of Yarmouth and Sangamon

interglacial age. I refer two metacarpals (UA*1643, 1644) from Saskatchewan gravels on the south bank of the Battle River, Alberta to *E. scotti* (Reimchen 1968, Table 13). They may be of mid-Wisconsin or earlier age. Evidently the species was common in southern and central Saskatchewan (Fort Qu'Appelle and Saskatoon) during Sangamon or mid-Wisconsin time.

In the Great Plains and Central Lowland provinces of the United States, *E. scotti* occurs in mammalian faunas of Kansan age from Rock Creek and other sites in Texas, from Holloman, Oklahoma and in the Cudahy fauna from both Kansas and Texas. It is also known from the early Illinoian of Kansas, and *E. cf. scotti* has been recorded from late Illinoian deposits in that state. During the Sangamon interglacial *E. scotti* and *E. cf. scotti* occupied the Slaton area in Texas and the Butler Spring area in Kansas, respectively. *E. scotti* is also known from Wisconsin deposits in Texas (Hibbard 1970, pp. 419-430).

Equus scotti was confined to North America. It first appeared on the western plains and spread rapidly, ranging from Alberta to Texas. Its ancestors are unknown. I speculate that it is related to early caballine horses, which may have originated in northern Asia - a

large form (*E. bresanus*) spreading to Europe in the Villafranchian (Kurtén 1968, p. 149) and a smaller form (e.g. *E. scotti*, and *E. cf. caballus* (Savage 1951, p. 239)) reaching North America via the Bering Isthmus in Kansan time. Its favored range seems to have been in Texas and Kansas during the middle to late Pleistocene. Apparently it shifted its range northward during the Yarmouth and Sangamon interglacials, perhaps reaching the Yukon during the latter phase. The lack of abundance of specimens of this kind of horse in the Yukon, and the fact that most fossils appear to be a late Wisconsin age, suggests that the species did not survive long there.

Equus scotti was a rather heavy set horse with a large head. Mature mares would have reached a height of about 15 hands (1.5 m). Its hooves were broader than those of living Arabian horses; however, in most characters it is very like modern horses (*Equus caballus*). The species may have lived in regions of "...luxuriant vegetation with plenty of food and water" (Troxell 1915, pp. 616-617). Rootlet markings on the surfaces of the metacarpal NMC 14485 and the metatarsal NMC 17573 may indicate that it occupied a grassland habitat in Eastern Beringia. It is interesting to note that it is associated with wild asses (*Equus (Asinus) sp.*) in a number of faunas

(e.g. early and late Illinoian faunas of Kansas; Sangamon faunas of Slaton, Texas, Cragin Quarry, Kansas, and Medicine Hat, Alberta; and Wisconsin faunas of Texas and the Yukon Territory). Perhaps they had broadly similar habitat requirements, but the wild asses mainly occupied drier portions of their mutual range. Probably large cats such as the American lion (*Panthera leo atrox*) and wolves preyed on *E. scotti*. Man may have hunted this horse, but no obvious kill sites similar to those found in Eurasia have been discovered.

Equus (Asinus) lambei (Yukon wild ass)

This was the dominant species of horse in the Dawson Area during the late Wisconsin. Many fossils comprising most parts of the skeleton, including a few good skulls, have been found there. In addition, remains of this small horse have been collected from the Sixtymile Area, Old Crow Area, and Herschel Island. In order to facilitate comparisons of the Yukon wild ass (Figures 50, 60A-B, 61A-D, 62A, 63A-B, Tables 64-68) with other species of Pleistocene and Recent wild ass, skull measurements are given, in addition to those of the metapodials. Descriptions and measurements of other skeletal elements are provided by Harington and Clulow (1973, pp. 708-724).

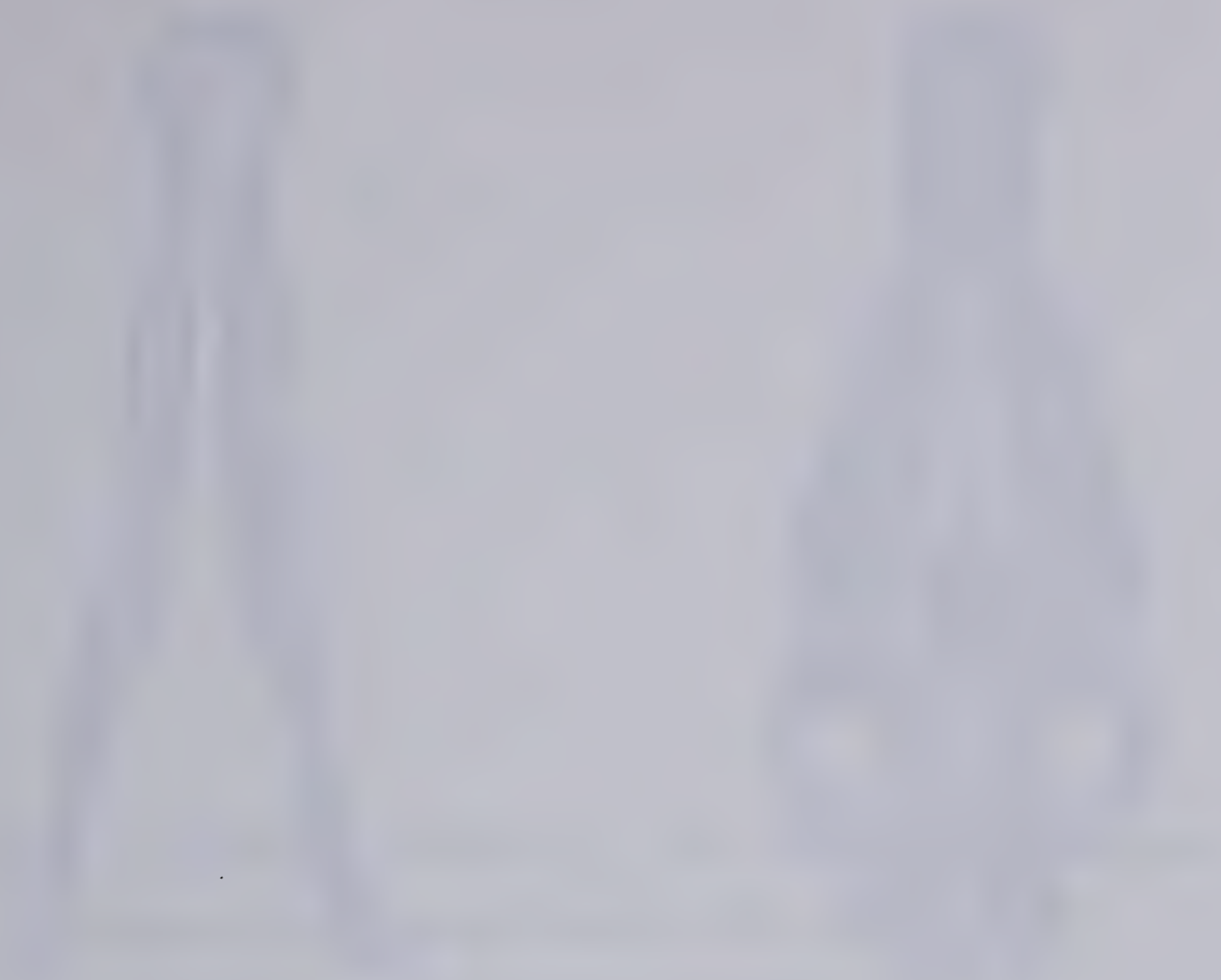
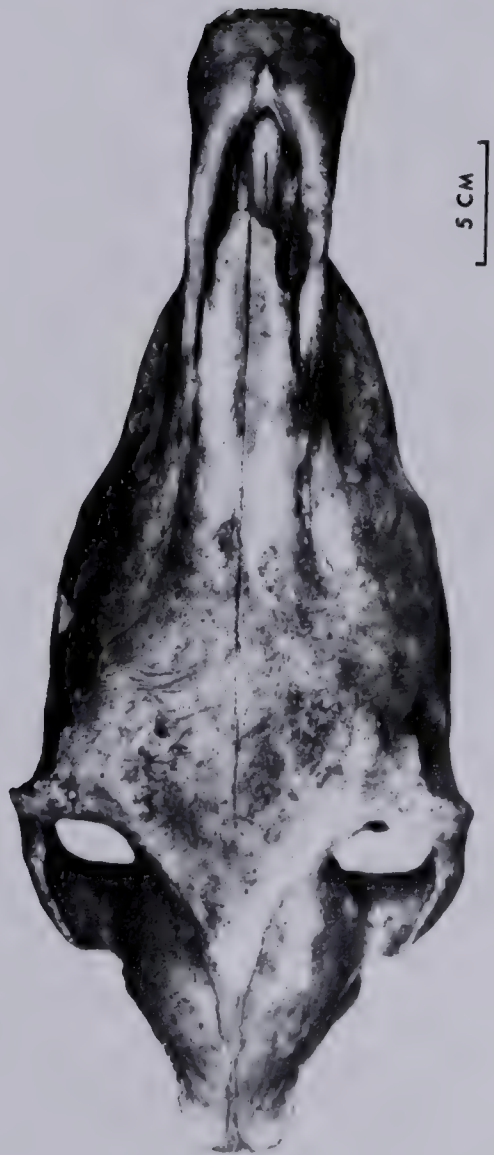


Figure 61. A. Dorsal view of mandible (USNM 8426, Dawson Locality 32) of the type of the Pleistocene Yukon wild ass (*Equus (Asinus) lambei*).
B. Ventral view of cranium (USNM 8426).
C. Right lateral view of complete skull (USNM 8426). D. Dorsal view of cranium (USNM 8426).



B



D



A



C



Figure 62. A. Occlusal view of right maxillary fragment with RP^2-RM^3 (NMC 29330, Old Crow Locality 146) of a Pleistocene Yukon wild ass (*Equus (Asinus) lambei*).

B. Occlusal view of a right upper cheek tooth (NMC 19034, Old Crow Locality 66) of a Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*).

C. Occlusal view of RM^3 (NMC 20830, Old Crow Locality 29) of a Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*).

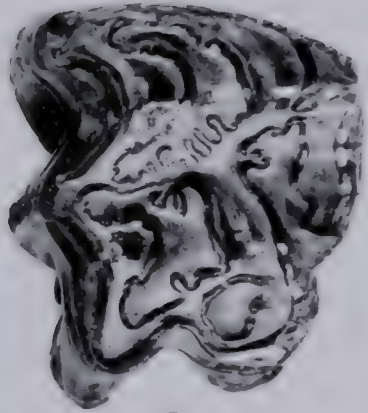
D. Occlusal view of right lower cheek tooth (NMC 26049, Old Crow Locality unknown) of a Pleistocene large horse (*Equus* cf. (*Plesippus*) *verae*).



A



B



C



D

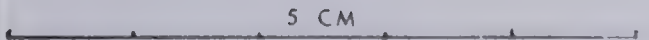


Figure 63. A. Anterior view of metacarpals (left to right LUM 1.91, 1.105, 1.92, 1.99, 1.100, 1.104, 1.95, 1.103, 1.175, 1.101; Dawson Locality 32) of the Pleistocene Yukon wild ass (*Equus (Asinus) lambei*), showing apparent bimodal grouping (see Figures 60A-B and Harington and Clulow 1973, Figure 26) into large male? specimens (right) and smaller female? specimens (left).

B. Posterior views (from left to right): right metatarsal (LUM 1.106, Dawson Locality 32) of a Pleistocene kiang-like wild ass (*Equus (Asinus) cf. kiang*); left metatarsal (NMC 13477, Dawson Locality 32) of a male? Pleistocene Yukon wild ass (*Equus (Asinus) lambei*); left metatarsal (NMC 13479; Dawson Locality 32) of a female? Pleistocene Yukon wild ass. (*Equus (Asinus) lambei*).



A
5 CM



B
5 CM

Table 64. Measurements of Pleistocene Yukon wild ass (*Equus (Asinus) lambei*) crania from the Yukon Territory.

SPECIMENS	PROBABLE SEX	ESTIMATED AGE	Measurements (mm) *																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
<i>Equus (Asinus) lambei.</i>																						
USNM 8426 Dawson Loc.32																						
(type)	Q	Adult	446	245	167	498	129	310	348	102	-	120	72	-	-	188	65	47	86	54	43	
LUM 1.222 Dawson Loc.32	Q	Adult	471	252	176	533	114	316	371	102	192	121	74	158	214	209	72	50e	89	54	51	
NMC 13485 Dawson Loc.32	+	2½ yrs.	450	246	168	504	125	295	-	101	-	114	-	157	-	-	61	45	86	-	43	
NMC 17262 Dawson Loc.28	Q	Adult	483	264	176	534	131	321	376	106	195	117	72	156	209	198	68	46	91	54	44	
NMC 17905 Dawson Loc.32	Q	Adult	496	265e	176	547	139	324	388	129	200	121e	-	159	210	205e	67e	52	106	65	45	
NMC 17235 Dawson Loc.28	Q	Old	476	269	172	542	133	325	384	115	204	117	-	164	217	207	72	55	97	63	52	
NMC 9924 Dawson Loc.12	Q	Adult	503	275	-	-	131	335	394	122	206	121	81	166	219	-	71	49	88	63	50	
NMC 17254 Dawson Loc.28	Q	Old	484a	262a	-	542a	133a	322a	383a	118	212	118	-	-	223	204	72	52e	98	66	50e	
NMC 13552 Dawson Loc.32	-	Adult	-	-	-	-	-	-	-	-	-	-	-	158	205*	-	-	43	-	61	-	

- * 1 - Middle of incisive border to anterior of foramen magnum.
 2 - Middle of incisive border to anterior of posterior nares.
 3 - Middle of incisive border to naso-premaxillary notch.
 4 - Middle of incisive border to posterior of occipital crest.
 5 - Middle of incisive border to anterior of PM².
 6 - Middle of incisive border to anterior of orbit.
 7 - Middle of incisive border to posterior of orbit.
 8 - Width across mastoid processes.
 9 - Width across articulation for lower jaw.
 10 - Width between outer faces of M³s.
 11 - Width between outer faces of I³s.
 12 - Minimum distance between orbits (anterior).
 13 - Maximum distance between orbits (posterior).
 14 - Middle of occipital crest to posterior of orbit.
 15 - Palatal width at M³s (minimum).
 16 - Palatal width at P²s (minimum).
 17 - Distance between I³ and P².
 18 - Anteroposterior diameter of orbit.
 19 - Least width between I³ and P² (on ridge).

Table 65. Measurements of Pleistocene Yukon wild ass (*Equus (Asinus) lambei*) upper dentitions from the Yukon Territory.

SPECIMENS	PROBABLE SEX	ESTIMATED AGE	MEASUREMENTS (mm) *																						
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21		
<i>Equus (Asinus) lambei.</i>																									
USNM 8426 Dawson Loc. 32 (type)	♀	Adult	36.0	28.0	12.0	25.5	28.0	17.0	26.0	29.0	17.0	22.5	27.0	14.0	24.4	27.0	16.0	27.0	24.5	19.0	167.0	87.0	77.0		
LUM 1.222 Dawson Loc. 32	♀	Adult	41.1	25.4	10.6	27.5	26.2	14.3	28.2	30.5	15.9	24.7	27.6	14.2	27.2	26.8	15.5	31.6	25.2	16.7	171.7	-	-		
NMC 13485 Dawson Loc. 32	♀	2½ yrs.	31.1	23.8**	10.8**	27.4	26.1	10.6	28.2**	25.3**	13.2**	30.7	27.6	15.1	31.4	25.2	14.1	-	-	-	-	-	-		
NMC 17262 Dawson Loc. 28	♀	Adult	37.1	26.4	9.6	29.1	29.8	12.7	28.1	30.3	13.5	25.4	28.0	11.8	25.3	27.2	12.9	26.4	23.0	13.9	175.2	95.9	82.5		
NMC 17905 Dawson Loc. 32	♀	Adult	37.7	23.6	8.4	27.8	26.9	10.6	25.8	28.0	11.2	22.6	26.6	11.9	24.1	24.7	12.1	30.5	22.3	13.7	167.0	90.8	79.1		
NMC 17235 Dawson Loc. 28	♂	Old	-	-	-	23.8	23.9	-	25.6	27.2	13.2	20.2	26.5	-	19.3	23.3	13.2	25.8	23.3	14.6	151.5	81.7	68.6		
NMC 9924 Dawson Loc. 12	♂	Adult	41.7	28.1	11.8	31.4	30.5	13.8	30.5	31.5	14.4	26.8	29.6	15.2	25.8	29.1	14.6	29.2	24.6	16.9	189.7	105.0	86.5		
NMC 17254 Dawson Loc. 28	♂	Old	38.0	23.2	11.0	25.6	28.4	16.4	25.0	29.0	16.3	21.6	26.2	14.2	21.8	27.0	14.2	26.2	24.5	16.9	156.1	84.9	72.6		
NMC 13552 Dawson Loc. 32	-	Adult	40.0	25.8	11.0	29.5	28.8	14.3	28.3	28.6	-	25.7	27.8	14.1	26.0	26.6	-	30.8	24.0	-	177.0	97.4	81.5		
NMC 29350 Old Crow Loc. 146	-	Adult	35.4	23.8	10.2	29.7	27.7	16.1	26.5	27.9	16.6	23.9	26.3	14.6	25.2	25.7	14.8	28.3	24.1	17.4	172.7	92.3	81.1		
NMC 13482 Dawson Loc. 32	-	Adult	-	-	-	29.2	28.3	14.9	28.9	29.2	15.8	25.2	26.8	13.5	26.2	26.9	13.4	27.2	24.0	14.7	175.2e	96.2e	82.0		
NMC 11628 Dawson Loc. 32	-	Adult	-	-	-	31.6	31.4	14.6	29.8	30.6	13.4	26.9	-	13.5	26.2	27.2	14.1	29.2	26.2	15.0	-	-	83.2e		

- | | | |
|-------------------------------------|--------------------------------------|---|
| * 1.. P ² length. | 8. P ⁴ width. | 15. M ² protocone length. |
| 2. P ² width. | 9. P ⁴ protocone length. | 16. M ³ length. |
| 3. P ² protocone length. | 10. M ¹ length. | 17. M ³ width. |
| 4. P ³ length. | 11. M ¹ width. | 18. M ³ protocone length. |
| 5. P ³ width. | 12. M ¹ protocone length. | 19. P ² -M ³ alveolar length. |
| 6. P ³ protocone length. | 13. M ² length. | 20. P ² -P ⁴ alveolar length. |
| 7. P ⁴ length. | 14. M ² width. | 21. M ¹ -M ³ alveolar length. |

**Measurement taken on milk tooth.

Table 66. Measurements of Pleistocene Yukon wild ass (*Equus (Asinus) lambelii*) lower dentitions from the Yukon Territory.

Specimens	Probable Sex	Estimated Age	Measurements (mm)*														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Equus (Asinus) lambelii</i> .																	
USNM 8426 Dawson Loc. 32 (Measurements from a plaster cast)	♀	Adult	31.6	18.2	26.2	19.4	27.3	19.7	23.0	18.3	26.2	17.5	32.1	16.8	169.2	85.6	83.4
LUM 1.222 Dawson Loc. 32	♀	Adult	34.3	16.3	27.6	18.1	27.4	19.2	23.4	17.6	24.2	17.5	35.5	16.2	171.1	-	-
NMC 9924 Dawson Loc. 12	♂	Adult	38.3	18.5	29.6	19.5	29.0	19.0	26.4	17.9	26.9	17.1	34.5	15.2	190.1	98.9	91.2
NMC 2778 Dawson Loc. unknown	♂	Adult	34.3	18.5	25.4	18.6	25.5	18.4	22.4	18.0	19.0	17.7	32.1	16.0	165.8	84.5	82.4
NMC 17255 Dawson Loc. 28	♂	Old	30.7	19.9	25.7	21.2	25.0	18.7	22.3	19.1	19.4	17.7	32.3	16.1	164.8	81.5	34.3
NMC 17261 Dawson Loc. 28	-	Adult	31.0	17.5	24.2	17.6	25.5	18.9	22.0	17.9	23.9	16.9	31.0	15.4	160.4	82.8	78.2
NMC 7748 Dawson Loc. 9	-	Adult	36.9	18.4	30.8	21.2	28.3	20.7	27.4	19.8	27.5	18.2	33.3	16.2	188.2	98.5	89.8

* 1 - P₂ length.2 - P₂ width.3 - P₃ length.4 - P₃ width.5 - P₄ length.6 - P₄ width.7 - M₁ length.8 - M₁ width.9 - M₂ length.10 - M₂ width.11 - M₃ length.12 - M₃ width.13 - P₂-M₃ alveolar length.14 - P₂-P₄ alveolar length.15 - M₁-M₃ alveolar length.

Table 67. Measurements of Pleistocene Yukon wild ass (*Equus (Asinus) lambei*) metacarpals from the Yukon Territory.

Specimens	Measurements (mm) *						
	1	2	3	4	5	6	7
<i>Equus (Asinus) lambei</i> , Pleistocene, Y.T.							
NMC 13472 Dawson Loc. 32	232.3	45.4	32.2	28.8	23.9	41.8	31.7
NMC 26009 Dawson Loc. 13	229.3	47.3	32.4	33.4	26.6	46.4	36.4
NMC 11631 Dawson Loc. 32	225.1	50.4	32.2	35.2	27.6	44.9	30.0 ⁺
NMC 25190 Dawson Loc. 16	224.8	50.2	-	36.0	26.6	48.8	-
NMC 29070 Sixtymile Loc. 3	224.5	46.6	32.7	31.8	25.5	45.4	36.7
NMC 29071 Sixtymile Loc. 3	224.4	49.1	33.6	34.8	25.9	43.8	34.1
NMC 28495 Old Crow Loc. 143	223.2	50.5	35.2	34.6	25.9	50.3	37.8
NMC 29231 Dawson Loc. 13	223.0	48.3	32.7	33.8	25.7	44.6	35.3
NMC 29073 Sixtymile Loc. 3	221.6	47.3	32.2	32.2	24.2	46.7	35.4
NMC 11630 Dawson Loc. 32	219.6	46.0	30.5	30.8	23.6	42.8	33.9
NMC 13474 Dawson Loc. 32	217.8	44.9	31.1	28.4	22.2	43.0	35.0
NMC 11757 Dawson Loc. 28	217.7	45.9	31.2	33.6	25.6	45.0	35.9
NMC 18040 Old Crow Loc. 11A	216.3	48.7	32.2	35.2	26.0	49.3	38.1
NMC 17267 Dawson Loc. 28	214.5	49.8	33.3	35.9	26.8	46.8	36.4
NMC 17057 Porcupine Loc. 100	212.2	49.2	29.2	33.8	25.2	47.5	36.5
NMC 16233 Old Crow Loc. 48	212.1	49.1	33.6	35.4	25.3	50.3	33.6 ⁺
NMC 13663 Old Crow Loc. 11A	211.3	47.9	30.3	32.7	24.4	47.2	36.1
NMC 11758 Dawson Loc. 28	210.7	44.6	28.0	33.5	26.3	44.1	29.8
NMC 13473 Dawson Loc. 32	210.2	46.6	31.7	32.7	26.1	43.8	36.3
NMC 17249 Dawson Loc. 28	209.8	45.3	31.6	30.3	24.2	43.5	34.2
NMC 29197 Dawson Loc. 8	209.7	44.3	30.1	31.9	24.1	40.6	32.5 ⁺
NMC 26008 Dawson Loc. 13	209.2	44.0e	27.5 ⁺	28.9 ⁺	25.1	40.6 ⁺	31.5 ⁺
NMC 17599 Dawson Loc. 28	209.1	44.4	31.2	31.8	25.8	45.6	35.5
NMC 25939 Dawson Loc. 16	208.0	45.1	31.1	29.7	24.1	43.4	33.1
NMC 17266 Dawson Loc. 28	207.8	41.3 ⁺	25.5 ⁺	30.9	23.5	40.2	28.4 ⁺
NMC 17598 Dawson Loc. 28	207.8	44.7	29.6	29.2	23.7	44.9	33.5
NMC 13475 Dawson Loc. 32	207.3	43.4	29.3	32.7	24.9	44.7	32.3
NMC 17584 Dawson Loc. 13	207.0	46.2	30.7	31.3	25.3	44.5	32.4
NMC 26723 Old Crow Loc. 20	206.3	49.0	31.6	32.6	23.4	46.4	35.6
NMC 24116 Old Crow Loc. 2	206.2	45.4	30.6	31.6	23.8	44.0e	33.4
NMC 11343 Dawson Loc. 2	205.4	44.9	29.6	30.3	23.3	42.1	33.2
NMC 25254 Dawson Loc. 8	204.8	44.9	31.1	32.9	25.4	44.3	34.2
NMC 11759 Dawson Loc. 28	204.6	42.2	25.9	29.6	22.2	36.1	26.3
NMC 25239 Dawson Loc. 32	204.6	43.2	30.3	30.7	24.2	45.6	34.0
NMC 23362 Old Crow Loc. 95	201.9	44.9	30.7	32.0	22.9	45.8	34.3
NMC 11756 Dawson Loc. 28	201.2	47.6	32.0	31.7	25.2	44.5	33.9
NMC 25247 Dawson Loc. 8	197.5	45.2	28.1	32.0	23.6	45.3	31.7

* 1 - Total length.
 2 - Proximal width.
 3 - Proximal depth.
 4 - Midshaft width.
 5 - Midshaft depth.
 6 - Distal width.
 7 - Distal depth.

Table 68. Measurements of Pleistocene Yukon wild ass

(Equus (Asinus) lambei) metatarsals from the Yukon Territory.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Equus (Asinus) lambei.</i>							
Pleistocene, Y.T.							
NMC 25938 Dawson Loc. 16	267.4	49.0	42.4	32.3	29.3	48.2	38.9
NMC 13476 Dawson Loc. 32	265.5	48.2	43.8	32.3	29.4	46.6	38.6
NMC 17563 Dawson Loc. 32	265.0	52.0	45.2	34.8	32.4	51.7	40.5
NMC 2773 Sixtymile Loc. 1	264.4	48.7	41.2	31.5	31.7	45.4	38.3
NMC 23375 Old Crow Loc. 11A	260.1	51.0	41.9	34.5	30.1	50.2	37.4
NMC 17270 Dawson Loc. 28	259.6	47.1	43.9	31.1	33.6	45.9	36.4
NMC 25178 Dawson Loc. 16	258.2	43.1	38.7	28.3	27.9	40.4	30.6
NMC 14667 Old Crow Loc. 26	257.7	51.3	42.9	35.7	37.2	52.3	36.1
NMC 13477 Dawson Loc. 32	256.0	48.6	40.1	34.6	29.9	48.3	36.6
NMC 10467 Dawson Loc. 24	255.9	46.5	39.8	32.3	30.2	46.6	33.3
NMC 25187 Dawson Loc. 16	254.2	50.4	42.6	31.9	31.2	50.9	37.7
NMC 25188 Dawson Loc. 16	253.0	42.6	38.1	27.1	27.1	40.8	32.1
NMC 11752 Dawson Loc. 28	252.0	49.3	40.5	33.4	29.7 ^e	47.3	34.3
NMC 29068 Sixtymile Loc. 3	251.0	47.4	39.0	30.9	29.0	46.0	35.5
NMC 13478 Dawson Loc. 32	249.5	44.2	37.2	30.5	30.1	43.3	35.0
NMC 17511 Dawson Loc. 32	249.0	42.9	35.8	29.3	29.1	43.4	33.7
NMC 17562 Dawson Loc. 32	248.4	44.5	38.5	31.7	29.3	45.6	36.4
NMC 28965 Dawson Loc. 17	248.2	47.3	38.6	32.4	29.1	46.1	35.6
NMC 11754 Dawson Loc. 28	247.4	44.5	37.5	30.6	29.6	43.1	33.7
NMC 13479 Dawson Loc. 32	245.2	44.5	37.6	30.0	28.9	45.8	35.6
NMC 11751 Dawson Loc. 28	244.4	42.9	38.3	31.0	29.8	44.7	34.7
NMC 13664 Old Crow Loc. 2	244.3	47.5	42.0	32.6	29.1	48.5	38.2
NMC 20492 Old Crow Loc. 20	244.1	48.7	42.3	32.5	28.7	50.0	37.6
NMC 26724 Old Crow Loc. 20	243.9	51.2	41.0	32.7	30.3	50.4	37.9
NMC 17585 Dawson Loc. 13	243.2	45.9	36.8	31.6	26.7	47.8	34.9
NMC 28966 Dawson Loc. 17	243.0	42.2	35.0	28.6	29.9	42.5	33.4
NMC 17917 Porcupine Loc. 100	242.9	48.7	41.7	32.1	28.9	45.8	-
NMC 24203 Old Crow Loc. 12	240.7	45.7	40.6	34.6	30.6	46.8	35.2
NMC 17600 Dawson Loc. 28	240.6	43.6	37.3	28.7	30.3	42.7	33.8
NMC 17269 Dawson Loc. 28	240.2	43.0	36.6	27.9	29.5	40.2	31.9
NMC 28968 Dawson Loc. 17	238.3	41.8	37.9	27.8	29.4	41.3	31.8
NMC 11753 Dawson Loc. 28	234.6	38.4	36.2	-	28.7	40.7	30.5

* 1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Midshaft width.

5 - Midshaft depth.

6 - Distal width.

7 - Distal depth.

As part of an attempt to organize sensibly the confused classification of North American Pleistocene horses, Savage (1951, p. 252) referred *E. lambei* to *E. cf. caballus*. Quinn (1957, p. 14), in a later revision, referred *E. lambei* to *Onager lambei* and listed additional specimens from Texas that he considered belonged to that species. Groves and Mazák (1967), after completing a comprehensive taxonomic study, placed Asiatic and African wild asses in the genus *Asinus*. They consider the name *Onager* Brisson, 1762 to be invalid, and list the more appropriate name *Hemionus* Stehlin and Graziosi, 1935 as a species, *Asinus hemionus*. Following Stirton (1942, pp. 636-637), I prefer to relegate *Asinus* to subgeneric level (as allowed for by Groves and Mazák (1967, p. 326)) and to consider the type specimen of the Yukon wild ass from Gold Run Creek near Dawson as *Equus (Asinus) lambei*. Thus, regarding the designation of the small, broad-skulled Yukon horse, I am inclined to disagree with Savage, while agreeing fundamentally with Quinn, and altering his nomenclature to conform in essence to that proposed by Groves and Mazák.

Referred specimens

The type specimen (USNM 8426 - not USNM 8226 as mentioned by Hay (1917)) consists of a complete cranium and mandible articulating with it, which evidently

belonged to a 12-year-old, or older, female. It was collected in 1903 by John M. Morrison at a depth of 32 feet (9.8 m) on claim 34 of Gold Run Creek (Dawson Locality 32). Hay (1917, p. 435) described and figured the specimen as the type of a new species of small horse *Equus lambei*. In searching the files of L.M. Lambe, I discovered a series of photographs of the type skull, taken for him by the Photographic Division of the Geological Survey of Canada in October 1912. Because of their unusual clarity compared to Hay's illustrations (1917, Plates 56-58), or because they show new views (or both) of this important specimen, a few are included. Although Hay (1917, p. 435) reported that LI^3 and LI_1 "have been lost since exhumation", they are present in Lambe's photographs.

Another excellent specimen of *E. (A.) lambei* from Dawson Locality 32 is a cranium with articulated mandible (LUM 1.222) collected in 1968 (Harrington and Clulow 1973, Figures 19-22). The cranium is complete except that it lacks the nasals, facial bone anterior to the right orbit, both I^1 s, and the tip of the right mastoid process. As the teeth are heavily worn and canines are not present, the specimen probably represents an old female. Thus, in age and sex the skull

is comparable to the type specimen USNM 8426. Like the type, protocones on the upper cheek teeth are long. Protocones on the heavily worn M^3 s are even narrower than those of the type (Hay 1917, p. 440). Groves and Mazák (1967, p. 324) remark that the protocone is generally elongated, especially posteriorly, in the Asiatic wild asses *Equus (Asinus) hemionus* and *Equus (Asinus) kiang*, and this observation applies to the teeth of *E. (A.) lambei*. The teeth of LUM 1.222 are very similar in shape and size to those of USNM 8426, but the cranium is substantially longer. In fact, the cranium of the type is the shortest known for the species. I believe such differences suggest the degree of individual variation that may be expected in the Yukon wild ass.

According to its stage of tooth eruption, the cranium NMC 13485 from Dawson Locality 32 represents an approximately $2\frac{1}{2}$ -year-old colt (Harrington and Clulow 1973, Figures 23-25). Canine regions are slightly swollen, but no teeth are evident, so NMC 13485 may represent a male or female. I include a detailed description of this specimen because it is chronologically younger than any previously known cranium of this species, and because it demonstrates clearly one stage in the sequence of maturation. Tips of I^1 s are visible;

dI^2 s and dLI^3 are present, but about to be replaced; dRI^3 is lost. LP^1 is present and has a well worn occlusal surface; RP^1 is missing. RP^2 is replacing dRP^2 , which is nearly worn to the roots and is slightly worn anteromedially. dLP^2 has been replaced by LP^2 , which projects through the gum line and has slightly worn paracones and protocone. P^3 s are replacing heavily worn dP^3 s. dLP^3 is worn away anteriorly and is almost ground to the roots posteriorly. dP^4 s are being replaced. M^1 s have well worn occlusal surfaces and project slightly above the level of the M^2 s. The occlusal surfaces of the M^2 s are only moderately worn, indicating recent eruption. RM^3 may have begun to erupt, but LM^3 has not broken the gum line. Although the latter tooth is present, the former evidently slipped dorsally out of its socket through a damaged area in the cranium and was lost. Most cranial sutures, including the basioccipital - basisphenoid suture, are unfused. Like the type specimen, NMC 13485 has long protocones on the permanent molars, a flat interorbital region, and a pronounced downward slant on the dorsal surface of the cranium between the middle of the braincase and the occipital crest. The occiput when viewed from above has the square, parallel-sided shape seen in *Equus (Asinus)*, rather than the rounded shape common in *Equus (Equus)* (Groves and Mazák 1967, p. 324).

The cranium NMC 17262 from Dawson Locality 28, lacking upper canines and having well worn incisors, probably represents an old female. Protocones on the posterior upper cheek teeth are long, and the enamel pattern on the upper cheek teeth is simple as in the type specimen. The cranium is complete except that the following bone is lacking: the tips of the nasals, the posterolateral part of the right nasal, the interior of the left orbit, most of the left parietal and part of the temporal, parts of the frontals, parts of the auditory bullae, and the tips of the paramastoid processes.

NMC 17905 from Dawson Locality 32 is a cranium lacking the incisors, LC^1 , RP^2 , LM^1-LM^3 , bone of the interior part of the orbits, most of the auditory bullae, and the right paramastoid process. The protocone on RM^3 is long and narrow as in the type specimen: the remainder are markedly shorter. As upper canines are present and the cheek teeth are worn (but still high from roots to occlusal surfaces), probably a mature male is represented. This specimen is 50 mm longer than the type. The bone is stained a rust color and has whitish patches. It tends to be chalky and rather fragile, probably due to long exposure and weathering. RM^2 is relatively small compared to those of most *E. (A.) lambei*.

seen. This tooth almost exactly matches a brownish stained ?RM² (NMC 18415) from Old Crow Locality 29. The latter specimen, which I refer to *Equus (Asinus) lambei*, has maximum crown dimensions of 24.1 mm long x 23.9 wide and has a very long protocone, while the RM² of the former is 24.1 mm long x 24.7 mm wide.

NMC 17235 from Dawson Locality 28 is a relatively broad cranium lacking the incisors and P³s. The canines are very heavily worn and the remaining cheek teeth are almost worn to the roots. Most sutures are well fused. Evidently this specimen represents an extremely old male. The tips of the nasals are lacking and the auditory bullae are badly damaged, as is the tip of the left paramastoid process. The dentition is interesting. Apparently RI³ was lost during life, and its alveolus was nearly completely filled by callus. The alveolar margins of the P² sockets are smoothed down, suggesting to me that the P²s were lost well before the animal died. M¹s are so heavily worn that hardly any enamel is apparent in the polished occlusal "basins". Another sign of old age is the porosity of the bone near the alveolar margins of the upper cheek teeth. Callus has also filled the areas posterior to the M³s where those teeth have "shrunk forward" (resulting in greatly decreased P²-M³ alveolar length) from their

situation during early maturity. Although most of the specimens are tan, NMC 17235 seems to have a blackish (manganese?) stain superimposed on top of the tan colored bone.

NMC 9924 from Dawson Locality 12 consists of most of a cranium lacking the dorsal region from a point between the orbits to the anterior part of the pre-maxillary nasal processes. Only the bone enclosing the roots of the cheek teeth and the upper part of the palate is seen when this part of the cranium is viewed from above. All teeth are present. The incisors are moderately worn and upper canines are present, indicating that the horse represented is an adult male. The occipital or nuchal crest is missing, as are the left lateral portion of the temporal condyle and orbital bone. A complete mandible containing all teeth was found with this cranium. It is the largest skull in the series.

NMC 17254 from Dawson Locality 28 consists of most of a cranium with all cheek teeth, LI^2 , LI^3 , LC^1 , and the socket for LI^1 . The cheek teeth, incisors and LC^1 show heavy wear. Probably the specimen represents an old male, but not so old as NMC 17235. Most of the

upper part of the cranium anterior to the frontals is missing, including the superior margins of the orbits. The right half of the cranium anterior to RP^2 is lacking. The bone surface is rather grainy due to heavy weathering. Small exostoseal growths occur posterior to M^3 s.

The degree of wear on the upper cheek teeth of a fragile cranium (NMC 13552) from Dawson Locality 32 indicates that it represents an adult. The specimen lacks the occipital area, part of the palate, and the region anterior to the cheek teeth. The right tooth row is complete, but the labial faces of RM^1 - RM^3 are badly chipped. LP^2 - LM^1 are present, but are poorly preserved. The cheek teeth are similar in size and simple enamel pattern to those of the type specimen.

NMC 29350 from Old Crow Locality 146 consists of a right maxillary fragment with RP^2 - RM^3 . The cheek teeth are moderately worn, so the specimen probably represents an adult. Because it is unusually complete compared to most Pleistocene horse fossils from the Old Crow Basin, because the bone is quite fresh in appearance (like most specimens from the late Wisconsin muck deposits of the Dawson Area), and because it is from the Pleistocene

vertebrate locality farthest up the Old Crow River, I consider NMC 29350 is evidence that herds of Yukon wild asses occupied the margins of the Old Crow Basin when it was last filled by Glacial Lake Old Crow during the late Wisconsin.

Other maxillary fragments with teeth have been recorded from Gold Run Creek (Dawson Locality 32). They represent adults according to the degree of wear on the cheek teeth. NMC 13482, a left maxillary fragment with LP^3-LM^3 , probably was derived from a slightly younger individual than NMC 11628. The latter specimen consists of a partial palate with nearly complete right tooth row. RP^2 , the labial margin of RM^1 and a lingual fragment of LP^4 are missing. Generally speaking, males seem to have consistently larger orbits and are broader across the mastoid processes than females.

It is worth noting that *E. (A.) lambei* mandibles differ from those of Recent horses (*E. caballus*) in the strong convexity of their ventral borders below the premolars. This difference is easily demonstrated by placing mandibles of *E. caballus* and *E. (A.) lambei* upright, side by side on a flat surface. The ventral border of the former species lies close to the surface

throughout its length, whereas the anterior part of the ventral border of the latter species rises well above the surface. Descriptions of a few of the most complete mandibles follow.

Measurements of virtually complete mandibles with all teeth, which articulate with the previously described crania (USNM 8426 and LUM 1.222 from Dawson Locality 32, and NMC 9924 from Dawson Locality 12) are included in Table 66. NMC 2778 from an unknown locality near Dawson consists of a complete mandible with teeth excepting LI_1 and RI_1 - RI_3 . Canines are well developed and incisors are heavily worn, suggesting that the specimen represents a male in late maturity. The tip of the right coronoid process is lacking and the condyles are slightly damaged. This specimen was purchased by D.D. Cairnes of the Geological Survey of Canada about 1916. NMC 17255 from Dawson Locality 28 evidently represents a slightly older male. The anterior cheek teeth are very heavily worn and the margins of the following teeth are missing: the anterior of RP_2 , the medial side of RP_4 , and the posterior portions of M_3 s. Most of the ascending rami are missing.

NMC 17261 from Dawson Locality 28 represents a younger horse than NMC 17255 or 2778. The specimen is

a left mandible lacking most of the diastema, the tip of the coronoid process and the medial end of the condyle. NMC 7748 from Dawson Locality 9 is the central part of a right mandible with all cheek teeth. The degree of wear on the cheek teeth indicates that the individual represented was mature at death. NMC 13553 from Dawson Locality 32 is a left mandibular fragment with LP_2 - LM_3 . It represents a mature individual. This specimen, like NMC 7748, lacks the diastema and ascending ramus.

The following metacarpals (III) are referred:

right - NMC 11631, 13475, 25239, 13472, 13474 (Dawson Locality 32), 17599, 11758-59, 17266 (Dawson Locality 28), 11343 (Dawson Locality 2), 17584 (Dawson Locality 13), 25247 (Dawson Locality 8), 29070 (Sixtymile Locality 3), 17057 (Porcupine Locality 100), 24116 (Old Crow Locality 2), 23362 (Old Crow Locality 95), 27406 (Old Crow Locality 129);
 left - NMC 29197, 25254 (Dawson Locality 8), 17249, 17598, 11756-57, 17267 (Dawson Locality 28), 26008, 29231 (Dawson Locality 13), 25991 (Dawson Locality 10), 25939, 25190 (Dawson Locality 16), 29071, 29073 (Sixtymile Locality 3), 13663, 18040 (Old Crow Locality 11A), 26723 (Old Crow Locality 20), 16233 (Old Crow Locality 48), 28495 (Old Crow Locality 143). NMC 13474 probably represents an individual that died during late immaturity because

the suture line is still visible where the distal epiphysis is fused to the shaft. It is one of the few Dawson bones that is dark brown. NMC 11756 and 17267 have metacarpal II fused to them, suggesting that they represent old individuals. Similarly NMC 17584 has metacarpal IV fused to it. Like the large horse (*Equus* cf. *Plesippus*) *verae*) metacarpal (NMC 14355) mentioned previously, NMC 13473 has an exostoseal lesion above the distal articulation (Choquette *et al.* 1975, Figures 2, 3). NMC 25190 and 11758 have been heavily gnawed by carnivores near the proximal and distal ends of the shafts, respectively. The following metacarpals have extensive rootlet impressions on their surfaces: NMC 23362, 13472, 29070, 11631, 29071, 17057, 13475, 25254, 25247, 11343, 11759, 17266. Metacarpals vary in total length from approximately 197 to 233 mm.

The following metatarsals (III) are referred:

right - NMC 13473, 17562, 17511 (Dawson Locality 32), 17270, 11752, 11751, 17600 (Dawson Locality 28), 28965, 28968 (Dawson Locality 17), 25188, 25178 (Dawson Locality 16), 29068 (Sixtymile Locality 3), 17917 (Porcupine Locality 100), 13664 (Old Crow Locality 2), 26724 (Old Crow Locality 20), 14667 (Old Crow Locality 26);

left - NMC 17563, 13477, 13479, 13478 (Dawson Locality 32),

11754, 11753, 17269 (Dawson Locality 28), 25938, 25187 (Dawson Locality 16), 28966 (Dawson Locality 17), 17585 (Dawson Locality 13), 24203 (Dawson Locality 12), 10467 (Dawson Locality 24), 2773 (Sixtymile Locality 1), 23375 (Old Crow Locality 11A), 20492 (Old Crow Locality 20).

Most of the specimens are light in color and fairly fresh looking, except for NMC 23375, 24203, 26724, and 13664 from the Old Crow Area, which are stained dark brown, and which may be of pre- late Wisconsin age. Abnormal proliferations of bone occur on the midshaft surfaces of NMC 25187 and 13477. The following metatarsals have clear networks of rootlet impressions on their surfaces: NMC 24203, 17562, 23375, 13477, 28966, 11751 and 25188. Such patterns may be indicative of death in a grassland environment. Metatarsals generally range in total length from 234 to 268 mm.

Discussion

Equus (Asinus) lambei was widespread in the Yukon during the ice age. Some of the fossils from both Old Crow and Dawson areas are suggestive evidence that Yukon wild asses occupied this part of Eastern Beringia before the late Wisconsin. The species seems to have been more abundant in the Dawson Area than in the Old Crow Area during the late Wisconsin, although it was definitely present on the western margin of the basin, probably when the last

Glacial Lake Old Crow was extant. A Yukon wild ass metapodial that I collected *in situ* near the base of the muck and the surface of the gold-bearing gravel on Dominion Creek (Dawson Locality 28) has yielded a radiocarbon date of approximately 15,000 years B.P., which tends to support the idea that Yukon wild asses survived in Eastern Beringia until the late Wisconsin.

Fossils of this species, or species like it, have been found in other parts of Canada. During the early 1970s, I identified *E. (A.) lambei* fossils from Pleistocene deposits in the Northwest Territories: (a) near Tununuk on the Mackenzie River in association with bones of a woolly mammoth (*Mammuthus* cf. *primigenius*) that gave a radiocarbon date of $19,440 \pm 290$ years B.P. (I-8578); (b) from Richard's Island at the mouth of the Mackenzie River; and (c) from the seafloor near a man-made island ("Immerk") used as an oil well platform (Harrington 1976 MS. p. 47). Ass-like horses are not uncommon in Sangamon to postglacial deposits of south-central British Columbia, Alberta and Saskatchewan (Harrington 1971a, p. 71; Stalker and Churcher 1970), but they are usually identified as belonging to the Mexican wild ass (*Equus (Asinus) conversidens*).

In the western United States, species belonging to *Equus (Asinus)* have been recorded from early Pleistocene (Late Blancan) deposits (e.g. "*Equus (Hemionus) calobatus*" from Sand Draw, Nebraska, and "*Equus (Asinus) cumminsi*" from Deer Park, Kansas, and Blanco, Texas (Skinner *et al.* 1972, p. 129)). *Equus (Asinus) conversidens*, the Mexican wild ass, did not appear on the North American plains until Illinoian time (Hibbard 1970, pp. 415, 423).

In Alaska, fossils of small Pleistocene horses have been reported from the Tofty area (Repenning *et al.* 1964, p. 183) - perhaps the type specimen of "*Equus niobrarensis alaskae*" from this region represents a male of *Equus (Asinus) lambei* - and from Lost Chicken Creek (Whitmore and Foster 1967; Harington 1976 MS. p. 75). A horse bone, probably that of a wild ass, from Lost Chicken Creek yielded a radiocarbon date of $26,760 \pm 300$ years B.P. (SI-355), which suggests that herds were present in that region just before the peak of the Wisconsin glaciation. Remains of small horses have also been recovered along the Ikpiuk River on the Arctic Coastal Plain (Harington 1976 MS. p. 75). Probably all of those specimens and most of the horse material from the Fairbanks area are referable to the Yukon wild

ass. Perhaps Jean Hough has identified one of the geologically earliest specimens of *E. (A.) lambei* in Alaska. It is most of a right mandible with teeth from terrace deposits of ?Illinoian age near Venetie (Péwé and Hopkins 1967, pp. 269-270).

Asiatic wild asses (*Equus (Asinus) hemionus*) lived in Siberia during the middle and late Pleistocene - in some cases with the arctic fox (Vangengeim 1961, p. 117). Remains of small horses, possibly asses like *Equus (Asinus) lambei*, have been collected from late Pleistocene (Illinoian to Wisconsin?) deposits as far north as the New Siberian Islands. They are usually referred to a small subspecies of *Equus caballus* by Soviet paleontologists (Vangengeim 1961, Figure 54b). Vereshchagin (1967, p. 391) states that wild asses were present in eastern Siberia during Paleolithic and Neolithic time. The relationships between Pleistocene horses of Siberia and the Yukon - Alaska region require careful consideration.

The kulan, a variety of Asiatic wild ass (*Equus (Asinus) hemionus kulan*), has been reported from several European localities in deposits of Riss (Illinoian) to Würm (Wisconsin) age. There is doubt about the exact identification of some of the specimens, however

(Kurtén 1968, p. 151). But Dietrich (1959) found both teeth and limb bones in Würm I-II (mid-Wisconsin) interstadial Rixdorf sediments at Berlin, definitely establishing the presence of *E. (A.) hemionus* there.

Although little is known about the dispersal history of the wild asses, possibly the earliest known species is *Equus (Asinus) stehlini* from the late Villafranchian of Italy (Groves 1974, p. 47; Kurtén 1968, p. 149). Evidently from Eurasia they spread eastward via the Bering Isthmus into southwestern North America during the late Blancan, and southward into Africa. Asses of the basic *Equus (Asinus) hemionus* type apparently first spread widely into the Holarctic northern steppe regions from Europe to the Yukon during the Illinoian glacial. They became the dominant horses of the Beringian arctic steppe during the late Wisconsin (Sher 1971, p. 153; Harington and Clulow 1973, p. 724). *Equus (Asinus) lambei* first occurs in deposits of ?Illinoian age in Alaska, and these Yukon wild asses seem to have lived in the Dawson and Old Crow areas of the Yukon, and in Alaska, in pre-late Wisconsin, as well as late Wisconsin time. Yukon wild asses survived in the Yukon until about 15,000 years ago.

I wish to stress the similarity among the skeletons

of *E. (A.) lambei* and its southern and western (Eurasian) relatives, *E. (A.) conversidens* and *E. (A.) hemionus*, respectively. Through the courtesy of C.O. Handley Jr. of the Smithsonian Institution, I have on loan a complete skeleton of a recent Asiatic wild ass *E. (A.) hemionus* (USNM 48493), the parts of which correspond closely to the same elements of the Yukon wild ass. However, the anterior upturn of the mandible, although present, is not so pronounced as it is in *E. (A.) lambei* mandibles described previously. Churcher (1968b, p. 1487) and Stalker and Churcher (1970) indicate the presence of *E. (A.) conversidens* in southern Alberta from Sangamon to postglacial time. The species evidently became extinct there about 8,000 years ago. Therefore, two asses, *E. (A.) lambei* and *E. (A.) conversidens*, lived in western Canada during the late Pleistocene and were separated at times by no more than 1,100 miles (1,770 km). Could these two forms be conspecific and closely related to, if not identical to, the Asiatic wild ass, *E. (A.) hemionus*? The zoogeographic and paleontological data, although somewhat sketchy at present, certainly do not preclude the conspecificity of these wild asses.

The Yukon wild ass formerly occupied the unglaciated areas of Alaska and the Yukon during the late

Pleistocene. It is extinct in America, but the possibility exists - should it be considered conspecific with *E. (A.) hemionus* - that it survives in Eurasia. The subspecies *Equus (Asinus) hemionus hemionus* or the *dziggetai*, which probably corresponds most closely to the Yukon wild ass, is presently found in southwestern Siberia, Transbaikalia and Dzungaria.

The Yukon wild ass was a small (about 1.3 m high), lightly built horse with a relatively large, broad head and long ears. It was probably buff in color with pale underparts, having a short black mane extending to a broad, dark dorsal stripe and a tail tipped with long black hair. The species was almost certainly capable of developing a thick (perhaps 20 cm long) winter coat, and in May probably looked very much like the excellent photograph of a moulting *dziggetai* provided by Groves (1974, p. 126).

Perhaps the Yukon wild ass had habits much like the living wild asses, favoring forb steppelands where snow is slight in winter, making grazing easier. The latter animals sometimes migrate long distances, and congregate in herds of up to 300, particularly in winter and summer, splitting up again in spring and autumn.

During most of the year, herds average 5 to 11 animals, consisting of an adult stallion, mares, two-year-olds and yearlings. The family herd is dominated by a stallion, but is usually led along by an old mare. Wild asses are fast (up to 64 km/hr) and can maintain that speed for several kilometres. They readily outdistance modern horses (*E. caballus*). They swim well and are able to climb rocky mountain slopes swiftly. During hot, dry periods they must drink regularly and watering places determine their summer distribution and daily behavior. However, in spring, when feed is more succulent, they obtain 10 to 15 litres of water daily without drinking.

The commonest items in their diet are sedges (e.g. *Carex*) and grasses, as well as various species of wormwood (*Artemisia* - known to have been common in the dry grasslands of Eastern Beringia during the Illinoian and Wisconsin glaciations) and saltwort (*Salsola*) (Solomatin 1973, Table 6). The commonness of rootlet impressions on many of the Yukon wild ass metapodials is suggestive evidence that the animals occupied grassy tracts. Perhaps this species is a good paleoenvironmental indicator of rather dry, shrub-covered grasslands.

In winter, wild asses may have to scrape through

the snow with their hooves to find food. They do not adapt well to deep, long-lasting snow. After heavy snowfalls they head for ravines and canyons where they often feed on shrubs. They are vulnerable to ice, which causes worn and bleeding hooves. During winter blizzards they cease grazing and move toward a sheltered spot in a valley or behind bushes, usually standing with their backs to the wind (Bannikov 1971).

Their speed and well developed senses of vision, hearing and smell help to protect them from predators. It is almost impossible for a person to get closer than 1 to 1.5 km without being noticed. In attack and defence they kick their victims with fore and hind hooves, stomp on them, and rip them with their teeth (Bannikov 1971). In Eastern Beringia during the late Pleistocene, probably only the fastest, craftiest predators such as the American lion and wolf were able to kill them (Figure 50). As yet, there is no evidence that they were hunted by early human occupants of the region.

Equus (Asinus) cf. kiang
(kiang-like wild ass)

Remains of these tall wild asses (Figure 63B, Table 69) are rare in Yukon Pleistocene deposits (Harrington and Clulow 1973, p. 724).

Referred specimens

A right metatarsal (LUM 1.106) from Dawson Locality 32 is unusually long and narrow compared to specimens referred to *Equus (Asinus) lambei*. The relatively large size of the specimen, and the fact that the epiphyses are fused to the shaft suggest that the fossil was derived from an adult. Comparison of LUM 1.106 with large and small *E. (A.) lambei* metatarsals (e.g. NMC 13477, 13479; Figure 63B) shows that: (a) the nutrient foramen on the posterior surface of LUM 1.106 is situated more distally; (b) facets for metacarpals II and IV are less developed on LUM 1.106, suggesting that they were relatively slender; (c) the distal articular surface of LUM 1.106 is relatively narrow and shallow, indicating the former presence of a smaller hoof; and (d) the non-articular depression on the proximal surface of LUM 1.106 is larger.

When compared in maximum length and proximal width to samples of some Recent and fossil horses, zebras and

Table 69. Measurements of Pleistocene kiang-like wild ass
(Equus (Asinus) cf. kiang) metatarsals from the Yukon
 Territory and Alaska compared to those of Recent kiangs
(Equus (Asinus) kiang) from Asia.

Specimens	Sex	Measurements (mm)*						
		1	2	3	4	5	6	7
<i>Equus (Asinus) cf. kiang.</i> Pleistocene, Y.T.								
LUM 1.106 Dawson Loc. 32	-	267.4	40.9	-	28.0	28.3	38.5	31.1
<i>Equus (Asinus) cf. kiang.</i> Pleistocene, Alaska								
NMC 25820 Lost Chicken Creek	-	269.0	43.4	38.1	28.0	28.4	40.4	32.8
<i>Equus (Asinus) kiang.</i> Recent, Asia**								
AMNH 57212 Right	♂	269.1	42.0	-	28.4	-	38.9	-
Left		267.0	42.0	-	27.3	-	38.6	-
AMNH 57214 Right	♂	270.0	40.5	-	26.5	-	40.5	-
Left		269.2	41.1	-	26.2	-	40.2	-
AMNH 57209 Right	-	269.5	42.0	-	27.7	-	40.4	-
Left		-	42.0	-	27.8	-	40.7	-
AMNH 57211 Right	♀?	266.6	40.4	-	25.8	-	37.8	-
Left		265.4	40.4	-	25.9	-	37.8	-
AMNH 60347 Right	♀?	270.8	40.1	-	27.2	-	37.8	-
Left		271.2	40.5	-	27.0	-	37.7	-
AMNH 57201 Right	♂	275.7	39.2	-	26.4	-	39.0	-
Left		275.0	39.7	-	26.3	-	39.2	-
AMNH 57208 Right	♂	276.0	43.9	-	26.5	-	39.6	-
Left		276.0	44.4	-	26.7	-	40.2	-

- * 1 - Total length.
 2 - Proximal width.
 3 - Proximal depth.
 4 - Midshaft width.
 5 - Midshaft depth.
 6 - Distal width.
 7 - Distal depth.

** M.F. Skinner kindly provided me with these measurements from specimens preserved in the Mammal Collection of the American Museum of Natural History, New York.

wild asses ("*Equus caballus*, *E. przewalski*, *E. grevyi*, *E. burchelli*, *E. calobatus*, *E. francisci*, *E. hemionus* {the kiang}, *E. asinus*"), LUM 1.106 is most similar to specimens of *Equus (Asinus) kiang* (= "*Equus hemionus kiang*", see Lundelius and Stevens 1970, Figure 3).

In 1974 I collected a left metatarsal (NMC 25820) from Lost Chicken Creek, Alaska of similar size and proportions to LUM 1.106. It is likewise referred to *Equus (Asinus)* cf. *kiang*, and is the first record of a kiang-like wild ass from the Pleistocene of Alaska. Other specimens may exist in the extensive Frick Collection from Alaska in the American Museum of Natural History (M.F. Skinner, personal communication 1974). NMC 25820 is very fresh in appearance, and I suggest that it is of late Wisconsin age. LUM 1.106 and NMC 25820 are best matched among a sample of living kiang metatarsals by AMNH 57212 (male), 57214 (male) and 57209 (sex unknown).

Discussion

Kiang-like asses occupied Eastern Beringia during the late Pleistocene - probably during the late Wisconsin, to be more specific. They seem to have been a much rarer element of the fauna than the Yukon wild asses, although their habits were undoubtedly similar in many ways.

In Canada, the only other specimen attributed to a stilt-legged wild ass is "*Equus ?calobatus*" from Kansan deposits at Medicine Hat, Alberta (Stalker and Churcher 1970), but it has not been described and therefore cannot be compared to the kiang-like wild ass.

In physical structure, *Equus (Asinus) cf. kiang* has its closest affinities among southern North American Pleistocene horses with *Equus (Asinus) francisci*. Concerning this matter, Lundelius and Stevens (1970, p. 150) state, "The metapodial elements of *E. francisci* are extremely long and slender, as indicated by the scatter diagram, and are most similar to those of Recent Asiatic asses, especially the kiang, *E. hemionus kiang*. The possibility exists, therefore, that *E. francisci* belongs to a North American kiang-like group. Another possibility, and the one favored by us, is that *E. francisci* is a southern, stilt-legged, ass-like equid which paralleled and surpassed Asiatic asses in metapodial elongation, but which had more generalized patterns of dental enamel and simple lower incisors. This position is supported by lack of close morphologic similarity between dentitions of *E. francisci* and Recent *E. hemionus kiang*." The type specimen of *E. (A.) francisci* (TAMU 2518) is from the Lissie Formation of Texas, which

is considered to be of Yarmouth interglacial age.

Fossils of this species are also known from the T-2 terrace of the Trinity River at Dallas, Texas, which is possibly of late Sangamon interglacial age. Because metatarsals of *E. (A.) francisci* average 15 mm longer and 7 mm narrower at the proximal end than those of *E. (A.) cf. kiang* from the late Pleistocene of Eastern Beringia, and because the latter specimens are well matched among living Asian kiangs, I suggest that they are more closely related to the kiangs of Asia.

Kiangs differ from Asiatic wild asses (*Equus (Asinus) hemionus*), and probably from Yukon wild asses (*Equus (Asinus) lambei*), in that they are somewhat larger (1.4 m high). Females weigh between 250 and 300 kg, while males often reach 400 kg. The species has a relatively large head, a thick muzzle and neck, a long upright mane, a short body and long limbs. The summer coat is reddish; the winter coat is browner and very long and thick (with underwool). There is a well-marked black dorsal stripe. The underparts are pure white. Kiangs presently occur in Tibet which, faunistically, is mainly a southern extension of the northern temperate zone fauna.

Kiangs live in herds that may vary in size from

5 to 10, occasionally up to 300 or 400. Adult males of 7 to 9 years tend to stay apart from the herds. Kiangs feed on grass and low vegetation, particularly the tough, sharp swamp grass, which would cut the more sensitive mouths of other horses. They put on fat in the "kiang-steppe" (very high, broad plains with xerophyllous vegetation) of Tibet during August and September. In winter, the streams freeze over, and kiangs break the ice with their hooves to get water. Later when the snow comes, they obtain moisture by eating it. They can swim well. Foals are usually dropped in late July or early August in rocky, protected places. Like Asiatic wild asses, kiangs have keenly developed senses. Apart from people, the kiang's only enemy is the wolf. Wolf packs follow the herds and separate young or sick animals, which are chased and overpowered (Groves 1974, pp. 86-96).

Perhaps this review will provide an insight into the habits of the kiang-like wild asses that occupied the Yukon and Alaska during the late Pleistocene. Kiang-like and Yukon wild asses may have been able to live sympatrically because of the greater adaptability of the former to feeding on the toughest plants, which the latter species largely neglected. Maybe "steppeization" of northern Eurasia and North America during the late

Pleistocene glaciations (Vangengeim 1967, p. 284; Hopkins 1967, p. 472) allowed both Asiatic wild asses and kiangs to reach North America via the Bering Isthmus.

Every effort should be made to solve this problem concerning the affinities and dispersal histories of the wild asses which occupied Eastern Beringia during the ice age.

Order Artiodactyla

Family Camelidae

Tribe Camelini (genus and species indeterminate)
(large camel)

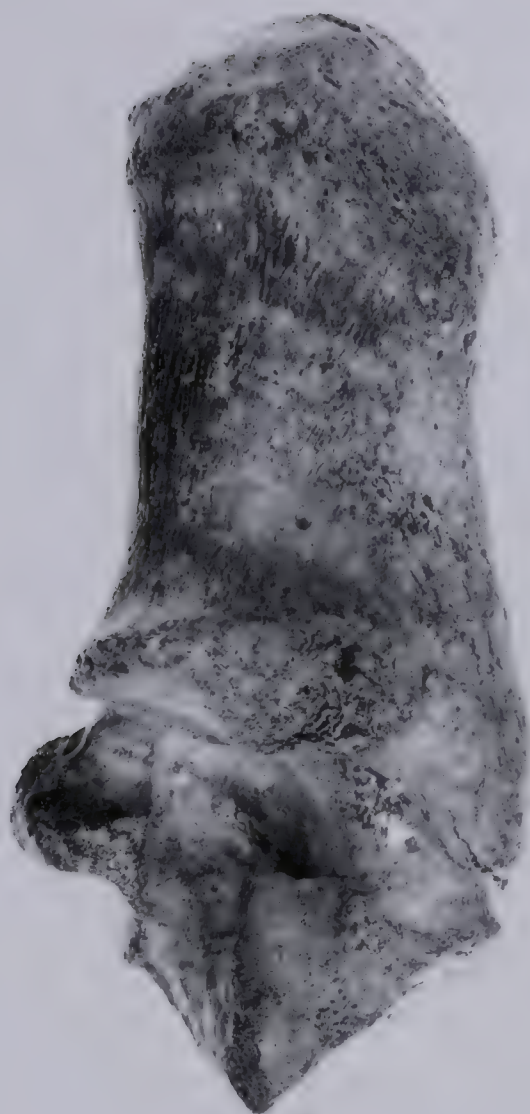
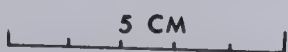
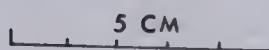
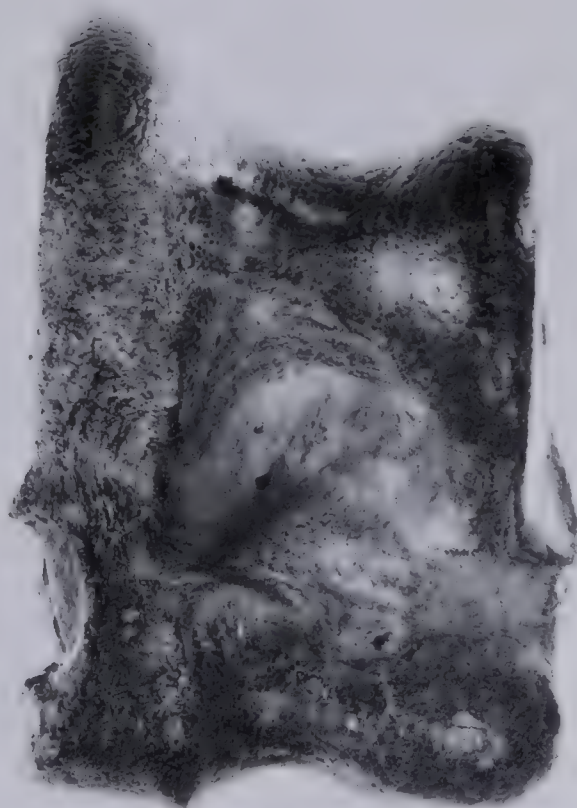
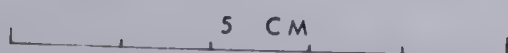
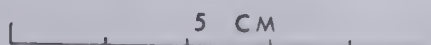
The first occurrence of a Pleistocene camel specimen north of the Arctic Circle in North America was reported by J.W. Gidley (1913, p. 1). While collecting Recent mammals for the Smithsonian Institution during the summer of 1912, Copeley Amory, Jr. obtained a small lot of Pleistocene mammal bones from a locality about 50 miles (80 km) upstream from the mouth of the Old Crow River. A single phalanx (NMC 8623 - a plaster cast of the original USNM specimen) of a camel was among the other bones, and was described by Gidley (1913, p. 2) as follows: "While this phalanx, a left of the proximal pair, is characteristically tylopoid and absolutely

unmistakeable as regards its group reference, it is not specifically determinable. It agrees approximately in size and proportions with the corresponding element in *Camelops kansasus* {*kansanus?*} Leidy, as that species is at present understood, but is flatter, and in this respect more nearly resembles the phalanges seen in the living genus *Camelus*." Thus, Gidley provided no generic or specific designation for the specimen, while noting similarities to phalanges of the Camelopini and Camelini.

Since Gidley's description, approximately 30 camel fossils, many of which are fragmentary, have been collected from Pleistocene deposits in the Old Crow Basin. Among these, a few teeth (particularly upper molars), several astragali, a calcaneum, and a few phalanges are sufficiently well preserved to be described (Figures 64A-D, 65A-B, D-E, Tables 70-73). These fossils are closest in shape and size to a very large member of the Camelini and are referred to a genus and species within that tribe. Of the two possible genera (*Camelus* and *Paracamelus* - unless a new genus is represented) to which the fossils may belong, a large species of *Paracamelus* seems the better choice according to comparative material and published data that I have examined. Pending



Figure 64. A. Anterior view of a right calcaneum
(NMC 13589, Old Crow Locality 11A) of a
large Pleistocene camel (Camelini).
B. Medial view of NMC 13589.
C. Posterior view of a right astragalus
(NMC 13590, Old Crow Locality 11A) of a
large Pleistocene camel (Camelini).
D. Anterior view of NMC 13590.

**A****B****C****D**

- Figure 65. A. Occlusal view of right upper molar (RM^2) (NMC 27486, Old Crow Locality 127) of a Pleistocene camel (Camelini).
- B. Occlusal view of left upper molar (LM^2) (NMC 20407, Old Crow Locality 22) of a Pleistocene camel (Camelini).
- C. Occlusal view of RM_3 (NMC 23285, Old Crow Locality 85) of a Pleistocene camel (tentatively referred to *Camelops* sp.).
- D. Anterior view of a second phalanx (NMC 14400, Old Crow Locality 21) of a Pleistocene camel (Camelini).
- E. Anterior view of a first phalanx (NMC 14775, Old Crow Locality 29) of a Pleistocene camel (Camelini).

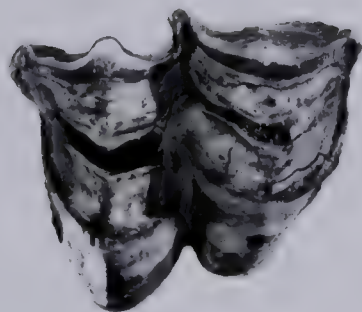
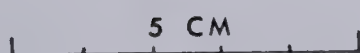
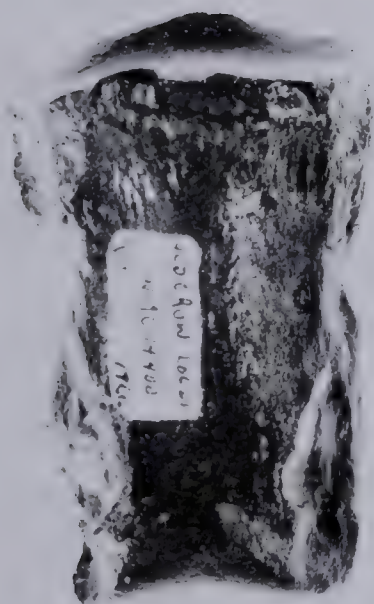
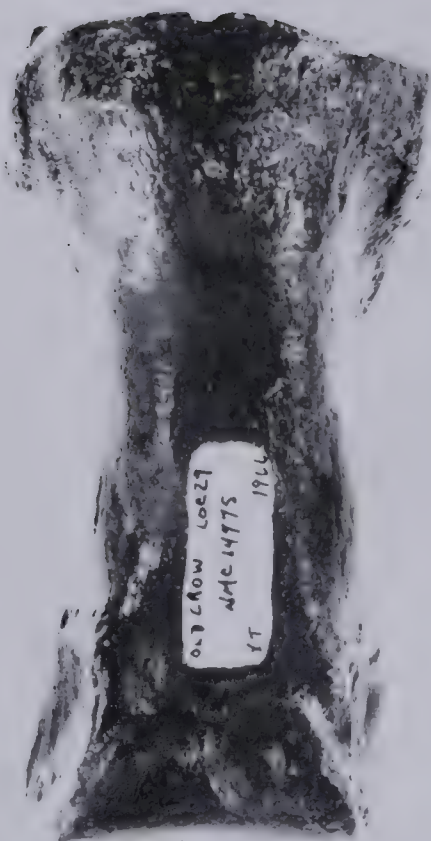
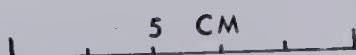
**A****B****C****D****E**

TABLE 70. Measurements of Pleistocene camel (Camelini) teeth from the Yukon Territory compared to those of *Paracamelus* from the Pliocene of China, Recent *Camelus*, and the Pleistocene western camel (*Camelops hesternus*) from California.

Specimens	Measurements (mm)*					
	1	2	3	4	5	6
<i>Camelini</i> . Pleistocene, Y.T.						
NMC 24213 Old Crow Loc. 66	35.8	27.8 ⁺	-	-	-	-
NMC 20407 Old Crow Loc. 22	-	-	50.4	37.7	-	-
NMC 27486 Old Crow Loc. 127	-	-	46.1	37.8	-	-
NMC 23268 Old Crow Loc. 11A	-	-	-	-	40.3	24.9
<i>Paracamelus gigas</i> . Upper Pliocene, China (Zdansky 1926, p. 11)						
Catalog number unknown	30.0	29.6	?46.0	42.4	34.7	?28.5
Catalog number unknown	-	-	50.0	41.0	-	-
<i>Camelus bactrianus</i> . Recent						
NMC 32202 Zoo specimen	24.5	27.0	48.9	32.2	38.5	23.1
<i>Camelops hesternus</i> . Pleistocene, Calif. (Webb 1965, Tables 5-6)						
UCMP 20028	19.7	23.8	39.2	30.8	28.2	19.9
UCMP 20040	28.0	22.5	51.9	32.8	38.7	21.5
LACM Z252	27.0	22.6	44.1	28.4	-	-
LACM Z256	50.4	20.3	54.5	28.2	-	-
LACM Z257	-	-	-	-	43.7	22.3
LACM Z263	-	-	-	-	34.9	21.0
LACM Z265	-	-	-	-	29.3	19.2

* 1 - P⁴ length. 2 - P⁴ width. 3 - M² length. 4 - M² width. 5 - M₁ length. 6 - M₁ width.

Table 71. Measurements of Pleistocene camel (*Camelini* and *Camelops hesternus*) astragali from the Yukon Territory compared to those of other Pliocene to Recent camels.

Specimens	Measurements (mm)*			
	1	2	3	4
<i>Camelini</i> .Pleistocene, Y.T.				
NMC 13590 Old Crow Loc. 11A	99.5	88.1	77.3	67.5
NMC 14100 Old Crow Loc. 11	103.6	95.1	79.9	67.0
NMC 19082 Old Crow Loc. 66	103.8	95.2	82.2	66.5
NMC 22951 Old Crow Loc. 66	99.2 ⁺	94.4	78.7	-
NMC 23568 Old Crow Loc. 11A	90.8 ⁺	93.0 ⁺	82.4	63.8 ⁺
NMC 20208 Old Crow Loc. 44	92.0 ⁺	-	-	-
<i>Paracamelus gigas</i> .Upper Pliocene, (Zdansky 1926, p. 33) China				
Catalog number unknown	98.0	88.5	75.5	62.0
<i>Titanotylopus spatulus</i> .Early Pleistocene (late Blancan) (Breyer 1974, Table 3) Nebraska Lisco C				
M	90.0	72.0	-	-
N	36	36	-	-
SE	0.88	0.70	-	-
<i>Camelops hesternus</i> .Pleistocene, Y.T.				
NMC 29194 Sixtymile Loc. 3	77.1	71.5	58.2	55.3
<i>Camelops hesternus</i> .Pleistocene (Webb 1965, Table 12) Calif.				
M	86.2 \pm 0.50	80.2 \pm 0.74	67.3 \pm 0.73	57.9 \pm 0.59
OR	80.5 - 91.9	75.2 - 85.3	62.4 - 72.5	55.3 - 64.6
N	18	18	18	18
SD	2.11	3.15	3.07	2.48
CV	2.35 \pm 0.39	3.93 \pm 0.66	4.56 \pm 0.76	4.30 \pm 0.72
<i>Camelus bactrianus</i> .Recent				
NMC 32202 Zoo specimen	74.9	68.8	56.0	50.2

* 1 - Length (lateral side). 2 - Length (medial side). 3 - Minimum length. 4 - Distal width.

Table 72. Measurements of a Pleistocene camel (*Camelini*) calcaneum from the Yukon Territory compared to calcanea of other Pliocene to Recent camels.

Specimens	Measurements (mm)*			
	1	2	3	4
<i>Camelini</i> .Pleistocene, Y.T.				
NMC 13589 Old Crow Loc. 11A	207.1	102.6	60.8	70.0
<i>Paracamelus gigas</i> .Upper Pliocene, China (Zdansky 1926, p. 33)				
Catalog number unknown	181.0	90.0	52.5	57.0
<i>Titanotylopus spatulus</i> .Early Pleistocene, (late Blancan) Nebraska (Breyer 1974, Table 2) Lisco C				
M	188.0	79.0	-	-
N	28	28	-	-
SE	1.77	0.76	-	-
<i>Camelus bactrianus</i> .Recent				
NMC 32202 Zoo specimen	139.9	71.4	41.2	44.2
<i>Camelops hesternus</i> .Pleistocene, Calif. (Webb 1965, Table 12)				
M	161.9 \pm 1.14	70.7 \pm 1.39	48.1 \pm 0.92	59.8 \pm 0.79
OR	157.0 - 170.0	65.0 - 76.7	40.5 - 53.2	56.4 - 65.3
N	13	13	13	13
SD	4.13	5.03	3.30	2.87
CV	2.56 \pm 0.50	7.10 \pm 1.39	6.85 \pm 1.34	4.80 \pm 0.94

* 1 - Maximum length.

2 - Maximum anteroposterior diameter.

3 - Transverse diameter of tuber calcis.

4 - Anteroposterior diameter of tuber calcis.

Table 71. Measurements of Pleistocene camel (Camelini) first and second phalanges from the Yukon Territory compared to those of other Pliocene to Recent camels.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
First Phalanges							
Camelini, Pleistocene, Y.T.							
NMC 27266 Old Crow Loc. 29	134.3	56.1	46.9	34.9	29.1	50.9	40.0
NMC 26957 Old Crow Loc. 23S	124.5	56.7	45.4	33.7	27.1	49.1	36.3
NMC 14775 Old Crow Loc. 29	121.0a	62.0a	-	33.0a	-	50.0a	-
NMC 8623 Old Crow - exact locality unknown (plaster cast of USNM specimen)	115.2	52.5	40.7	34.1	25.2	44.8a	34.4a
<i>Paracamelus gigas</i>, Upper Pliocene, China (Zdansky 1926, pp. 20, 33-34)							
Forelimb - Catalog number unknown	130.0	46.0	45.0	-	-	-	39.0
Hindlimb - Catalog number unknown	121.0	48.0	38.5	-	-	39.3	32.0
<i>Titanotylopus spatulus</i>, Early Pleistocene (late Blancan) (Breyer 1974, Table 1) Nebraska Lisco C							
M	119.0	57.0	-	-	-	-	-
N	80	80	-	-	-	-	-
SE	1.43	0.72	-	-	-	-	-
<i>Camelus bactrianus</i>, Recent NMC 32202 Zoo specimen							
Forelimb	100.3	41.6	34.0	20.8	20.6	38.9	29.8
Hindlimb	91.3	37.8	29.7	18.6	17.7	34.3	26.5
<i>Camelops hesternus</i>, Pleistocene, Calif. (Webb 1965, Tables 10, 12)**							
Forelimb M	122.3 ± 1.62	47.3 ± 0.97	38.9 ± 1.20	-	-	39.9 ± 0.71	33.9 ± 0.71
OR	117.0 -	44.0 -	36.0 -	-	-	38.0 -	32.0 -
N	127.0	52.0	45.0	-	-	42.0	37.0
SD	7	7	7	-	-	7	7
CV	4.30	2.56	3.18	-	-	1.87	1.87
M	3.51 ± 0.94	6.88 ± 1.62	6.45 ± 1.52	-	-	6.95 ± 1.64	4.66 ± 1.10
Hindlimb M	108.4 ± 1.19	45.2 ± 1.04	38.7 ± 0.83	-	-	36.6 ± 0.85	31.1 ± 0.48
OR	103.0 -	42.0 -	36.0 -	-	-	34.0 -	29.0 -
N	114.0	51.0	43.0	-	-	42.0	34.0
SD	9	9	9	-	-	9	9
CV	3.56	3.11	2.50	-	-	2.54	1.45
M	3.28 ± 0.78	6.88 ± 1.62	6.45 ± 1.52	-	-	6.95 ± 1.64	4.66 ± 1.10
Second Phalanges***							
Camelini, Pleistocene, Y.T.							
NMC 14400 Old Crow, Loc. 21	82.7	50.2	38.9	38.3	27.8	46.4*	30.6a
<i>Paracamelus gigas</i>, Upper Pliocene, China (Zdansky 1926, pp. 20, 33)							
Forelimb - Catalog number unknown	774.0	737.0	27.0	-	-	741.0	-
Hindlimb - Catalog number unknown	69.0	31.0	21.0	-	-	38.5	-
<i>Camelus bactrianus</i>, Recent NMC 32202 Zoo specimen							
Forelimb	65.6	31.6	27.4	25.8	17.0	37.2	18.5
Hindlimb	61.8	31.1	26.3	24.9	18.0	36.2	19.5

* 1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Midshaft width.

5 - Midshaft depth.

6 - Distal width.

7 - Distal depth.

** Presumably the forelimb measurements were accidentally switched with those of the hindlimb in *Camelops hesternus*, for Webb (1965, p. 32) states, "The phalanges of the hind foot are slightly smaller than in the fore foot."

The tabular data are corrected here.

*** Measurements of second phalanges are not given for *Titanotylopus spatulus* by Breyer (1974) or for *Camelops hesternus* by Webb (1965).

comparison of the Yukon fossils with actual specimens of *Paracamelus*, I prefer to leave their generic and specific designation in abeyance. *Paracamelus* has not been reported previously from North America.

Referred specimens

Three incisors have been collected. NMC 19068 from Old Crow Locality 66 is a slightly worn RI_1 lacking most of the root. A 15 mm-long facet with vertical striae occurs on its anteromedial surface, suggesting that I_1 s rubbed up and down against each other - probably when food was being nipped or torn up by the camel. NMC 19068 is approximately 22 mm wide and 56 mm long. The enamel is stained black. NMC 15428 from Old Crow Locality 14N is a complete, slightly worn LI_3 . It is approximately 18 mm wide and is 75 mm long. The enamel is black and the root is reddish brown. NMC 28386 from Old Crow Locality 134 is a complete, heavily worn RI_3 . It is about 19 mm wide and 77 mm long. The enamel is of dark ivory color; the root is stained dark brown.

Among the cheek teeth, only the following relatively complete specimens are described. NMC 24213 from Old Crow Locality 66 is an RP^4 lacking portions of the anterolingual and posterolabial surface enamel. It is doubtfully referred to the Camelidae. It appears to be slightly

larger than a P^4 of *Paracamelus gigas* and is much larger, especially in length, than P^4 s of a Recent Bactrian camel (*Camelus bactrianus*, NMC 32202) and Pleistocene western camels (*Camelops hesternus*). An interesting feature of this tooth is the broad plication that enters the lingual part of the fossette - a feature that Webb (1965, p. 43) has noted in all specimens of *Megatylopus matthewi* which were available to him. I do not know if this character has been reported in *Paracamelus*. It requires further comparison with large cervid P^4 s, as it also bears resemblance to this tooth in *Alces latifrons* (Kahlke 1956, Vol. II, Figure 22). The tooth is stained black.

NMC 20407 from Old Crow Locality 22 is an LM^2 . Its size and the heavy wear on the occlusal surface indicate that it represents an adult. NMC 27486 from Old Crow Locality 127 is an RM^2 . Like NMC 20407 it is well worn, lacks most of the roots, has grayish enamel and brown-stained dentine, and is similar in size to M^2 s of *Paracamelus gigas*. These molars are markedly broader than M^2 s of the Bactrian camel and *Camelops hesternus*.

NMC 23268 from Old Crow Locality 11A is an RM_1 . It is well worn, has grayish black enamel and is larger than most other camel M_1 s to which it was compared (Table 70).

Six astragali, obviously derived from very large camels, are in the collection. The best preserved is NMC 13590 from Old Crow Locality 11A. It is a right astragalus that articulates well with a right calcaneum NMC 13589 found at the same locality in the same year. NMC 13590 is very close in size to an astragalus of *Paracamelus gigas*, and to the type astragalus of *Megatylopus major* from Alachua Clays of Tertiary age from Florida that measures 99.5 mm long x 66.0 mm in distal width. Further, the lateral articular facets of NMC 13590 match almost exactly those illustrated by Zdansky (1926, Figure 15), except that no groove is seen between the parasustentacular and sustentacular facets. Evidently a narrow one is present in *Paracamelus gigas* which extends farther back than in NMC 13590, but which does not completely separate the two facets. This groove is also present in *Camelus* and is very broad and deep in *Titanotylopus spatulus* from the Lisco localities in Nebraska (J. Breyer, personal communication 1975). In medial view the Yukon specimen closely resembles astragali of *Titanotylopus spatulus* (Breyer 1974, Figure 4A). From a dorsal view, the sustentacular surface of NMC 13590 is like that of *Paracamelus*: both are much broader than that of *Camelus*.

Other right astragali include: NMC 14100 from Old Crow Locality 11, which is pitted on the sustentacular surface and has tough, sandy matrix adhering to depressions on the lateral surface; and NMC 23568 from Old Crow Locality 11A, which has been severely damaged by a carnivore gnawing on the anterior and posterior ends.

Left astragali include: NMC 19082 from Old Crow Locality 66 - the largest of the fossil astragali preserved, and larger than any of *Paracamelus gigas* or *Titanotylopus spatulus* mentioned by Zdansky (1926, p. 33) or Breyer (1974, Table 3), respectively; NMC 22951 from Old Crow Locality 66, which is badly eroded; and NMC 20208, excavated from the top of the organic subunit of Unit 1 at Old Crow Locality 44, which may be of late Illinoian or early Sangamon age. Generally, these astragali have dimensions larger than the means of any *Paracamelus*, *Titanotylopus*, *Camelus* or *Camelops* astragali to which they were compared (Table 71).

The single right calcaneum, NMC 13589 from Old Crow Locality 11A, is in good condition except for slight damage to the posterior part of the sustentaculum. The specimen is close in size and shape to calcanea of *Titanotylopus*, except that the convexity beneath the

sustentaculum is slightly less than in the fossils from Lisco, Nebraska (J. Breyer, personal communication 1975). I can see no difference between NMC 13589 and clear photographs of five views of a left calcaneum of *Paracamelus gigas* (M 1548) from Zdansky's collection from the Pliocene of China. I am grateful to N.J. Mateer of the Paleontological Institute of Uppsala University for supplying the prints. A calcaneum (possibly M 1548) of *P. gigas* measured by Zdansky averages approximately 15% smaller than NMC 13589, and the mean of a series of *Titanotylopus* calcanea from the early Pleistocene of Nebraska averages nearly 16% smaller.

Casts of the astragalus NMC 13590 and the calcaneum NMC 13589 were sent to S.D. Webb and J. Breyer for identification. I am most grateful for their comments. Webb (personal communication 1975) agreed with me that the fossils did not belong to *Camelops*, but a larger camelid, stating, "They may well belong to *Paracamelus* or *Camelus* extensively recorded across Northern Asia (especially Siberia) and into Eastern Europe." Breyer (personal communication 1975) concludes: "I would not hesitate to say that the specimens are from a member of the Camelini. As to the generic assignment I am not certain. The calcaneum and the general size

suggest *Titanotylopus*. The astragalus is another matter. Both the calcaneum and the astragalus have the form of the same elements in *Camelus*, but the size difference is considerable. I have never examined postcranial elements of *Paracamelus*, certainly it cannot be ruled out." Therefore, on the basis of these two fossils Webb and Breyer agree that a member of the Camelini is represented.

Three distal metapodial fragments are preserved. NMC 20856 from Old Crow Locality 74 includes the "fork" between ?metatarsals III and IV, and the medial half of the distal end of one of these ?metatarsals, including part of the articular surface. The anteroposterior diameter of the articulation is 49.1 mm, while the length from the top of the "fork" to the extremity of the distal articular surface is 79 mm - over twice the "fork" length of the metapodials in Recent *Camelus bactrianus* (approximately 36 mm). NMC 27501 from Old Crow Locality 66 and NMC 20278 from Old Crow Locality 75 are distal articular ends of metapodials. The latter is too heavily damaged to obtain reliable measurements. The former has a distal width of 52.1 mm and a distal depth of 70.0 mm. This compares to distal widths and depths of 46.0 mm and 48.5 mm (metatarsal IV) and 54.0 mm and 55.0 mm (metacarpal III) in *Paracamelus gigas* (Zdansky 1926, pp. 20, 33).

A few first phalanges are referred to a large member of the Camelini. It should be noted that there seems to be no way of distinguishing phalanges of the hindfoot from those of the forefoot except that the latter tend to be slightly larger. The relatively large size of NMC 27266 from Old Crow Locality 29 suggests that it is from a forefoot. Its surface is pitted in places, as if it had been attacked by acid in the groundwater. NMC 26934 from Old Crow Locality 23S, a distal fragment of a first phalanx, is slightly larger than the same part of NMC 27266, and is probably from the forefoot, too. NMC 26957 from Old Crow Locality 23S and NMC 14775 from Old Crow Locality 29 are of similar size. Both are stained dark brown. NMC 8623 from a locality some 50 miles (80 km) up the Old Crow River is smaller than the other specimens, and the measurements provided for *Paracamelus gigas*. Nevertheless, I consider it, NMC 26957 and 14775 as probably representing first phalanges of the hindfoot, for they average 10% smaller than NMC 27260 - approximately the relationship of forelimb to hindlimb first phalanges in *Paracamelus gigas*, *Camelops hesternus* and *Camelus bactrianus* (Table 73).

The first phalanges of the large Yukon camel are similar in length and depth to one of *Paracamelus gigas*,

but they are broader. As in *Titanotylopus spatulus* (Breyer 1974, p. 76, Figure 2) the posterior surfaces of all Yukon first phalanges can be divided into three nearly equal segments: (a) the proximal, covered by rugosities of the suspensory ligaments and indented centrally from below by a smooth wedge, the edges of which are termed "arms"; (b) a smooth central portion; and (c) the distal trochlear portion. It is worth noting that the emarginations below the proximal portion display "arms" of subequal length like *Titanotylopus* - except for NMC 26957, which has "arms" of unequal length like those of *Hemiauchenia* (= *Tanupoloma*) (Breyer 1974, p. 75, Figure 2c). I suspect, therefore, that this feature is to some extent variable in the large Yukon camel. *Camelops* can be readily separated from the large Yukon camel, *Titanotylopus* and *Hemiauchenia* on characters of the posterior surface of the first phalanx, for in *Camelops* the rugose area for the attachment of the suspensory ligaments extends half way down the shaft; nor is the distal border of the roughened proximal portion indented by a smooth wedge.

NMC 14400 from Old Crow Locality 21 articulates well with the large first phalanx (NMC 27266), and probably represents a second phalanx of the forefoot.

According to measurements given by Zdansky (1926, p. 20), a second phalanx of the forefoot of *Paracamelus gigas* is between 10% and 30% smaller than the Yukon specimen.

Discussion

All of the large Yukon camel bones are stained brown to blackish brown, and are probably of pre- late Wisconsin age. The astragalus (NMC 20208) excavated from the top of Unit 1 at Old Crow Locality 44 indicates that this species may have lived in the Yukon until late Illinoian or early Sangamon time, if the specimen had not been reworked from older sediments. Remains of large camels other than those attributed to *Camelops* have not been recorded previously from Eastern Beringia.

Fossils of various camels, mainly referred to *Camelops* or *Hemiauchenia*, have been reported from deposits of Kansan to Wisconsin age at Medicine Hat, Alberta (Stalker and Churcher 1970; Harington 1976 MS. pp. 31-41), but no large members of the Camelini resembling *Paracamelus* have been recorded there. However, Reimchen (1968, pp. 14-15, Table 2) has described a distal articular fragment of a metapodial (UA* 1622) having a distal width of 61.0 mm and a distal depth of 51.0 mm (slightly larger than NMC 20278), which he refers to *Titanotylopus* sp. The specimen was derived from Saskatchewan gravels in

northwest Edmonton, Alberta, which Reimchen (1968, p. 41) suggests are of Yarmouth or earlier age.

The camels (Subfamily Camelinae) originated from a *Protolabis*-like ancestor during the Miocene. That stock gave rise to three tribes which have probably evolved separately since Barstovian time: the Lamini (*Pliauchenia*, *Hemiauchenia*, *Paleolama*, *Lama*); the Camelopini (*Megatylopus*, *Camelops*); and the Camelini (*Procamelus*, *Titanotylopus*, *Paracamelus*, *Camelus*).

The Camelini had its origins in North America with *Procamelus* of the late Miocene to middle Pliocene. Evidently *Titanotylopus* stemmed from *Procamelus* in the middle Pliocene and survived until the mid-Pleistocene. It was confined to North America - particularly the western parts. *Procamelus* was also ancestral to the Eurasian camels (*Camelus* and *Paracamelus*).

Camelus occupied western Siberia, the Black Sea area, and the lower Volga (*Camelus bactrianus knoblochi*) during the middle Pleistocene, and Armenia (*Camelus dromedarius dahl*) during the late Pleistocene. It is also known from the Pleistocene of Europe, and North Africa. Bactrian camels occur naturally in small

numbers in the Gobi Desert, while dromedaries are used domestically from North Africa to India (Burton 1965, p. 194). Apparently *Camelus* arose from *Paracamelus* in the upper Pliocene (*contra* Webb 1965, Figure 22) (Gromova 1968, p. 496).

Paracamelus to which genus the large Yukon camel may belong, or to which it may be closely allied, is known from the upper part of the middle Pliocene to the early Pleistocene of Asia. Specifically, *P. gigas* and *P. praebactrianus* are recorded from the middle or upper Pliocene of the northern Caucasus, northern Kazakhstan, western Siberia and the Irtysh region; *P. alexejevi* is recorded from the middle Pliocene of Odessa and southern Moldavia; *Paracamelus* is also recorded from the Middle Pliocene to lower Pleistocene of northern China, Mongolia, the Soviet Union, Rumania and Hungary. A dwarf subgeneric group (*Neoparacamelus*) occurs in Pliocene to lower Pleistocene deposits near the Black Sea (Khaveson 1954; Gromova 1968, p. 499). Presumably the ancestors of *Paracamelus* crossed the Bering Isthmus from North America to Asia in the early to middle Pliocene. Perhaps the large Yukon camel fossils are the remains of this Beringian "missing link", or more likely a later Pleistocene form derived from it that was able to survive until late

Illinoian or early Sangamon time in this rather isolated northern pocket.

Paracamelus was approximately 16% larger than the living Bactrian camel and it had a long, narrow skull. Zdansky (1926, p. 35) states that, apart from its significantly larger size and massiveness, it is difficult to distinguish *Paracamelus gigas* from the living camels. A complete skeletal mount of the smaller *P. alexeevi* in the Museum of the Geological Institute of the Ukranian Academy of Science, Kiev provides a good idea of the conformation of this animal (Khaveson 1954, Plate X).

Presumably *Paracamelus* occupied arid steppe grasslands in interior continental regions. Modern camels are able to grow extremely thick pelts under cold environmental conditions. I have seen Bactrian camels at ease, wandering over snow-covered terrain in mid-winter at the Alberta Game Farm near Edmonton, and Sanderson (1955, p. 248) states that Bactrian camels may be encountered "plodding stolidly through north-Asiatic winter blizzards...". Undoubtedly *Paracamelus* and the large Yukon camel were well adapted to surviving under cold conditions. Perhaps *Paracamelus*, like living camels, commonly fed on dry scrub, and providing it had sufficient water at intervals, could

travel great distances.

Little is known about the natural predators of camels. Marks on the astragalus NMC 23568 indicate that it was gnawed by a medium to large-sized carnivore. The gnaw marks appear to have been made when the bone was fresh. The animal responsible for the marks could have killed the camel, or may have been a scavenger that attacked the carcass after the camel died.

Camelops hesternus (western camel)

Remains of the western camel (Figures 65C, 66A-B, Table 71) are very rare in Pleistocene deposits of the Yukon Territory.

Referred specimen

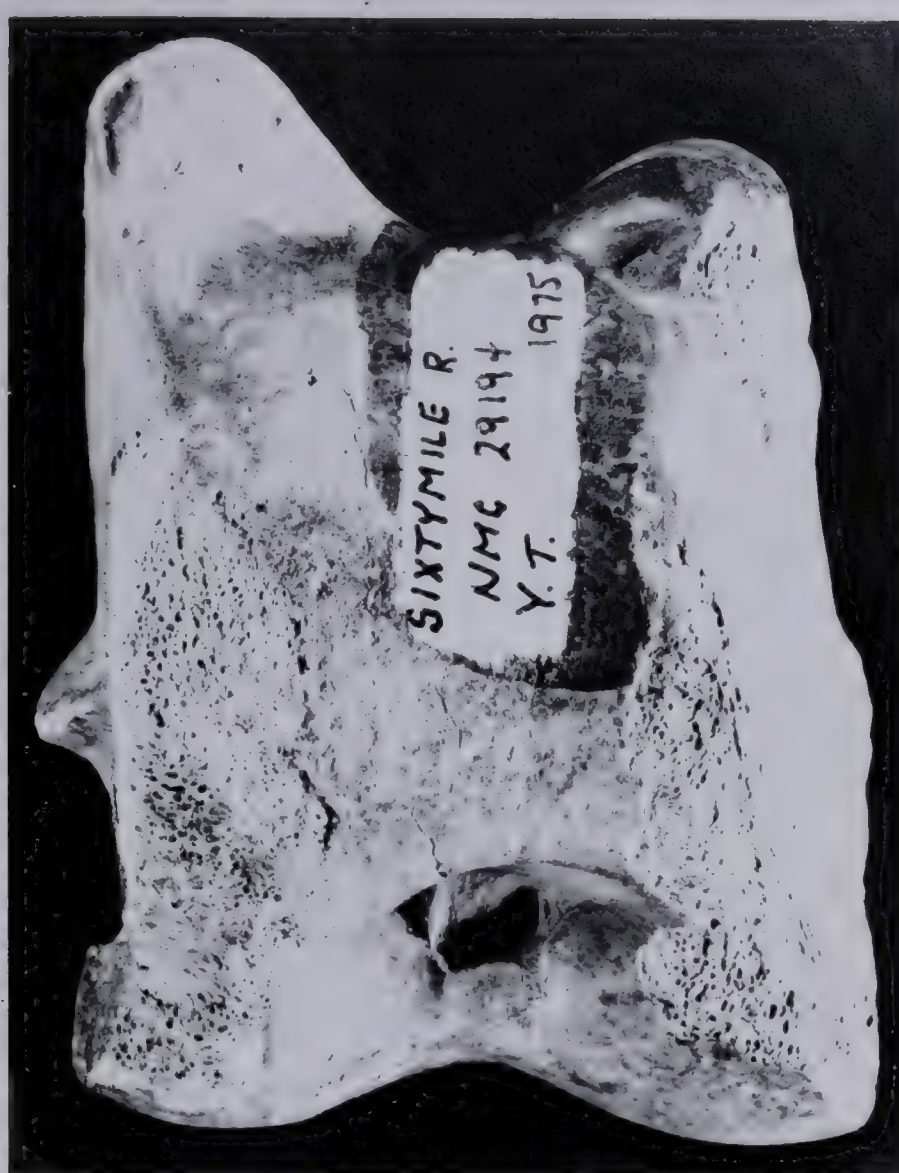
Only one specimen can be definitely referred to this species. It is a left astragalus (NMC 29194) from Sixtymile Locality 3 showing signs of erosion on the medial and lateral margins of the sustentacular facet. On the average, it is 21% smaller than an astragalus (NMC 13590) of a large Yukon camel referred to the *Camelini*. In most measurements NMC 29194 is between 3 and 5 mm smaller than the smallest specimens in a sample of 18 astragali of *Camelops hesternus* from late Pleistocene deposits at Rancho La Brea, California, but is 4 mm greater in lateral length than the mean



Figure 66. Left astragalus (NMC 29194, Sixtymile
Locality 3) of a Pleistocene western camel
(*Camelops hesternus*).

A. Posterior view.

B. Anterior view.



A

5 CM



B

5 CM

of a sample of 62 *Camelops* astragali from three faunas of Irvingtonian land mammal age (Gordon, Hay Springs and Rushville) (Breyer 1974, Table 3). It is slightly larger than an astragalus of Recent *Camelus bactrianus* (NMC 32202), but appears to match closely good line drawings and photographs of *Camelops hesternus* astragali (Webb 1965, Figure 15; Breyer 1974, Figure 6C-D).

The valley of the proximal trochlea of NMC 29194 forms a more acute angle than in astragali of the large Yukon camels, and the medial trochlear crest seems to be more pronounced than in a figured specimen of *Camelops hesternus* (Webb 1965, Figure 15). A posterior projection between the fibular salient and the distal astragalar facet is better developed than in the large Yukon camel astragali. This projection shows clearly in a photograph of *Camelops* provided by Breyer (1974, Figure 6D).

The angle of obliquity of the tibial ligament surface relative to the plane of the medial articular facets appears to be important in differentiating astragali belonging to different camelid taxa. The angle is more acute in the Yukon western camel NMC 29194 (27°) than in either the large Yukon camel (average 42.5°)

or Recent *Camelus bactrianus* (50°). It is interesting to note that in *Hemiauchenia*, the tibial ligament surface is parallel to that of the medial articular facets (Breyer 1974, p. 80). It may be worth pursuing a study of all camelids in this respect, in an attempt to discern whether or not large samples of astragali representing different groups could be separated. Functional reasons for differences observed could also be examined.

NMC 29194 is light brown, and is fresher in appearance than any of the camel fossils from the Old Crow Basin. This specimen from the Sixtymile fauna is probably of late Wisconsin age, according to the affinities of that fauna with faunas from Gold Run Creek near Dawson and Lost Chicken Creek, Alaska (Harrington 1976 MS. p. 63).

NMC 23285 from Old Crow Locality 84 is an RM_3 lacking roots and the posteriormost cusp. It is of similar size and shape to *Camelops hesternus* M_3 s described by Webb (1965). The degree of wear on its occlusal surface suggests that it represents an animal in early maturity. Because the tooth is fragmentary, slightly worn, and because I have not been able to compare it directly with M_3 s of *Camelops hesternus*, it is doubtfully referred to the western camel and the Camelidae.

Discussion

Evidently very few western camels occupied the unglaciated part of the Yukon Territory during the late Wisconsin: perhaps they were there for a relatively short time. The species reached the Yukon from southern North America.

In Alaska, fossils referred to *Camelops* have been reported by Frick (1930, p. 79), Geist (1953, p. 172; 1956, p. 201) and Guthrie (1968b, p. 353; 1972, p. 296, chart) from the Fairbanks area. Repenning identified *Camelops* remains with an assemblage including small horse, bison, mammoth, mountain sheep, wolf, hare and ?caribou from Canyon Creek near Big Delta (Webber 1975, p. 67). These specimens have not yet been formally described. The only radiocarbon date on *Camelops* sp. from Eastern Beringia is from the ?Fairbanks area. Analysis of collagen from a metapodial yielded a date of $24,900 \pm 1,100$ years B.P. (I-2117) (J.V. Matthews, Jr., personal communication 1975), indicating that the species was living in central Alaska near the peak of the Wisconsin glaciation.

In Canada, apart from the Yukon Territory, finds of *Camelops* are, so far, restricted to Alberta and Saskatchewan. The earliest report is of *Camelops* sp.

from early Pleistocene (Aftonian) deposits at Wellsch Valley, Saskatchewan. *Camelops minidokae* is recorded from the lowest Pleistocene (Kansan) mammal-bearing stratum represented near Medicine Hat, Alberta. In addition, this genus is recorded from a series of progressively younger deposits there (e.g. *Camelops* sp. of Yarmouth interglacial age; *Camelops hesternus* - Sangamon interglacial; *Camelops* cf. *hesternus* - early Wisconsin, early mid-Wisconsin, late mid-Wisconsin; *Camelops* sp. - late Wisconsin). A proximal phalanx probably referable to *Camelops* was collected in eastern Edmonton, Alberta, and *Camelops* cf. *hesternus* of late Wisconsin age has been reported from Empress, Alberta. In Saskatchewan, *Camelops* cf. *hesternus* and *Camelops* sp. are known from deposits of Sangamon interglacial or Wisconsin interstadial age at Fort Qu'Appelle and Saskatoon, respectively (Harrington 1976 MS. pp. 24-40).

Camelops remains are common in the United States. Although Webb (1965, p. 44) lists the earliest occurrence of the genus as late Pliocene, I can uncover no records earlier than those from Cita Canyon, Texas and Sand Draw (Keim Formation), Nebraska, which are considered to be of early Pleistocene (late Blancan) age (Hibbard 1970, Table 3; Skinner *et al.* 1972, p. 114, Figure 60). The genus is represented in the Borchers fauna (Aftonian

interglacial) of Kansas (Hibbard 1970, Table 5; Skinner *et al.* 1972, Figure 60). *Camelops* is relatively common in Kansan age faunas of the Great Plains and Central Lowland provinces, such as: Gilliland and Rock Creek, Texas; Holloman, Oklahoma; and the Cudahy fauna of Kansas and Texas. During early and late Illinoian time, this camel occurred in Kansas, and in the following Sangamon interglacial phase it was present at Slaton, Texas and Cragin Quarry, Kansas (Hibbard 1970, Tables 6-7). Among many other Wisconsin age faunas, *Camelops* is recorded from various localities in New Mexico, Texas and Kansas.

In summary, *Camelops* first appeared in southern North America during the early Pleistocene (late Blancan). It evidently stemmed from *Megatylopus*, which occupied approximately the same region throughout the Pliocene (Webb 1965, p. 44). Apparently *Camelops* first penetrated the southwestern plains of Canada (Wellsch Valley) during the Aftonian interglacial and was relatively common there and in the western United States until late Wisconsin time. Perhaps during the Sangamon interglacial it was able to spread northward to Eastern Beringia, where it lived at least until the peak of the Wisconsin glaciation. Establishing the age of the fossils in stream channel fill at Canyon Creek, Alaska may be of critical importance to

discovering when *Camelops* first entered Eastern Beringia. In southern North America, *Camelops hesternus* became extinct toward the close of the last glaciation. Webb (1974b, p. 207), in commenting on the absence of *Camelops* in Florida during the Pleistocene, remarks: "It now seems unlikely that *Camelops* even ranged into eastern North America." I speculate that the reason for the inability of this genus to flourish there was because the area was wetter than the plains and largely dominated by forest. Presumably for the same reason, fossils of the American lion (*Panthera leo atrox*) have never been recorded from northeastern North America. It seems to have been a carnivore adapted to open grassland or parkland.

Camelops hesternus was confined to North America. In life, it probably looked very much like a large (7 feet (2.1 m) to the top of the back) dromedary (*Camelus dromedarius*). A good restoration is provided by Webb (1965, Frontispiece) and a photograph of a mounted skeleton in the Los Angeles County Museum is given by Stock (1965, Figure 21). Its limbs were 20% longer, its leg joints knobbier, and its head was longer and narrower than those of the dromedary. Although the base of the neck was very low, the head was normally carried high. The tall neural spines and lack of lumbar spines suggest that

the western camel had a single mid-dorsal hump situated somewhat farther forward than in the dromedary. In *Camelops hesternus* the toes were not as fully encased in a pad or as broadly flattened as in the Bactrian camel or the dromedary. Mummified remains of this species have been found in a cave near Fillmore, Utah, with dried muscle still attached to the skull (Romer 1928, p. 19).

During the Pleistocene, large herds of *Camelops* roamed the western parts of North America. Such finds as dozens of well preserved specimens of Wisconsin age excavated from the tar pits at Rancho La Brea, California, tend to support this statement. Although primarily adapted as a grazer, the long neck and limbs of *Camelops hesternus* were probably advantageous for occasional browsing (Webb 1965, p. 33). It appears to be a good paleoenvironmental indicator of arid scrublands and grasslands, and the Yukon and Alaskan occurrences suggest that it could tolerate cool, at times snow-covered, steppe grasslands.

Association of western camels with Paleo-Indians is claimed at the following archeological sites: Sandia Cave, Burnet Cave, and Clovis, New Mexico; Paisley Cave, Oregon; the Lindenmeier site, Colorado; Tule Springs,

Nevada; and Double Adobe, Arizona (Martin and Guilday 1967, p. 46). Bones of this species have also turned up in the main occupation level at Jaguar Cave, Idaho, which has been radiocarbon dated at $10,370 \pm 350$ years B.P. (Kurtén and Anderson 1972, Table 16). However, no archeological kill sites are known. Perhaps American lions were able to prey on these fleet-footed camels.

Family Cervidae

Cervus elaphus (wapiti)

Several wapiti specimens (Figures 67A-B, 68A-C, Tables 74-76) have been collected from Yukon Pleistocene deposits. Most fossils are from the Dawson Area, and all seem to be of late Wisconsin age.

Referred specimens

One of the best specimens is a shed left antler (DCMP-3) from Sulphur Creek near Dawson. It lacks the tips of the third (supernumerary), fifth and seventh tines. Its surface detail is well preserved. The fossil is large compared to antlers of living wapiti, for if it were measured by Boone and Crockett Club standards - providing it had a uniform mate - it would be a new world's record. The specimen has been illustrated, but not described in detail, by Guthrie (1966, p. 50, Figure 2). A feature of this specimen that characterizes some Alaskan Pleistocene wapiti



Figure 67. Posterior cranial fragment with antler
pedicels (NMC 6750, Dawson Locality 5) of
a wapiti (*Cervus elaphus*).

A. Dorsal view.

B. Left lateral view. Anterior is to
the left.

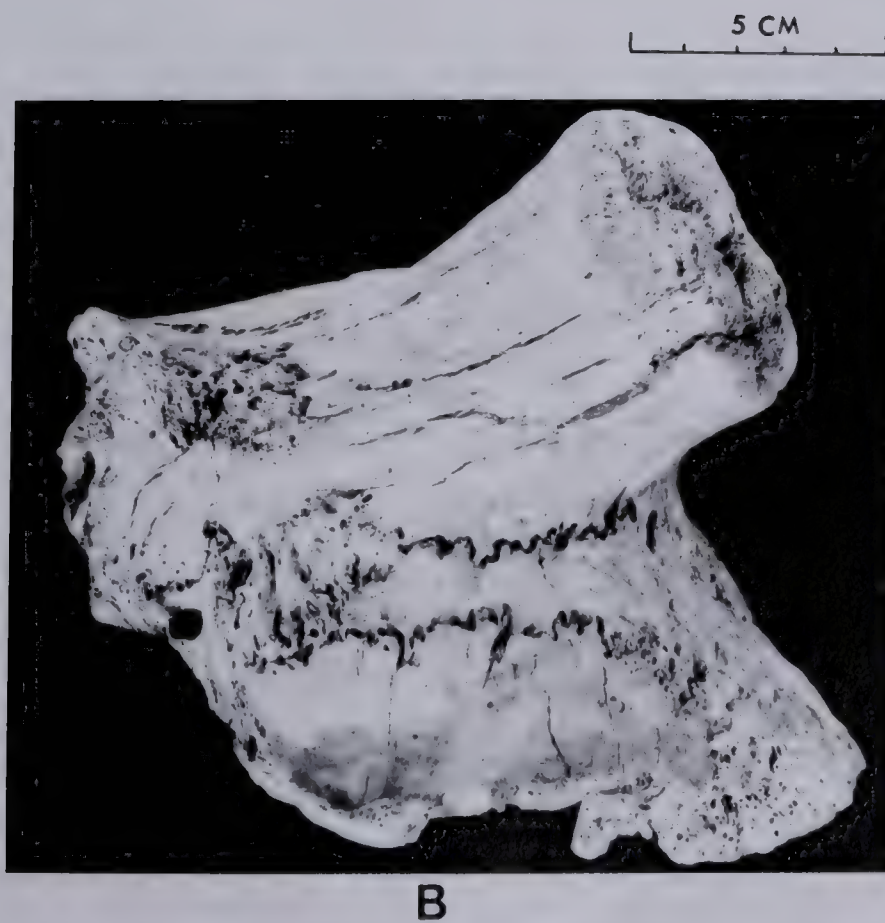
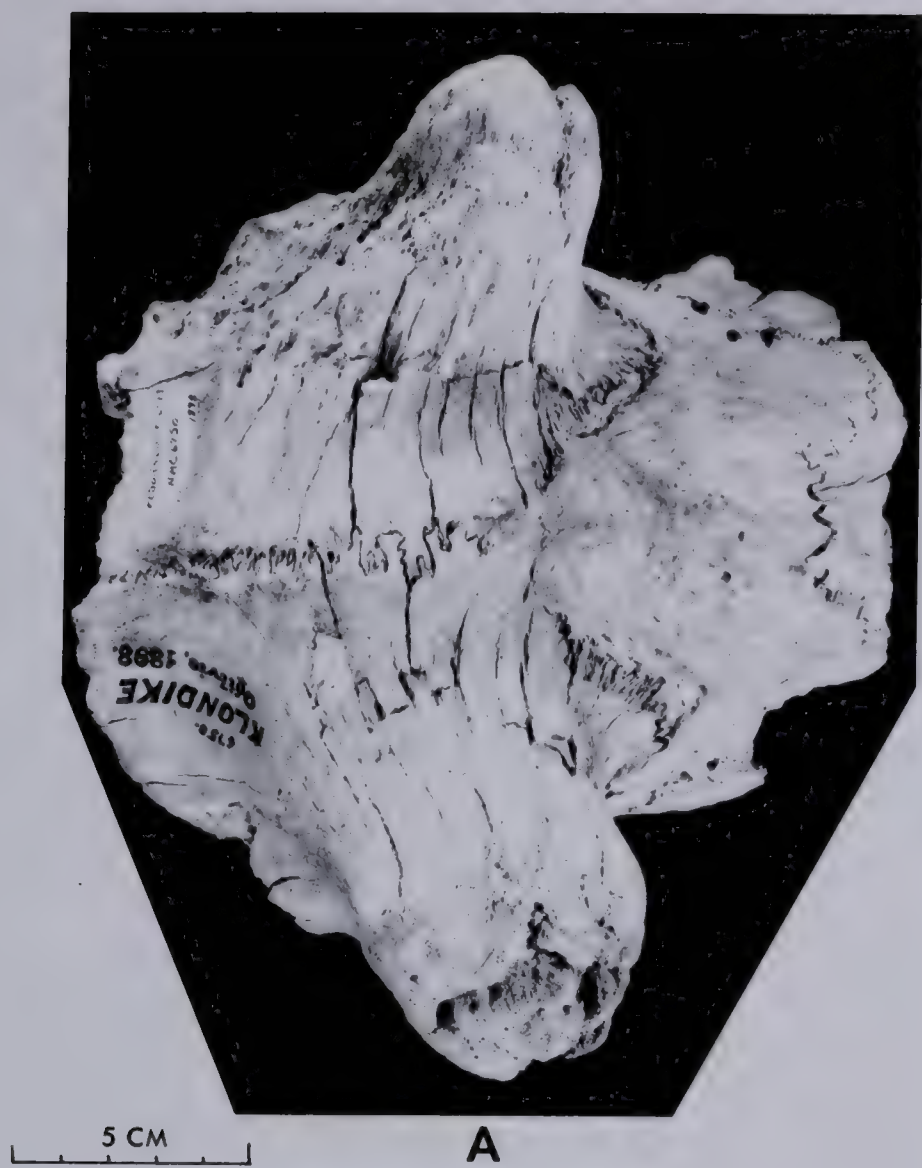
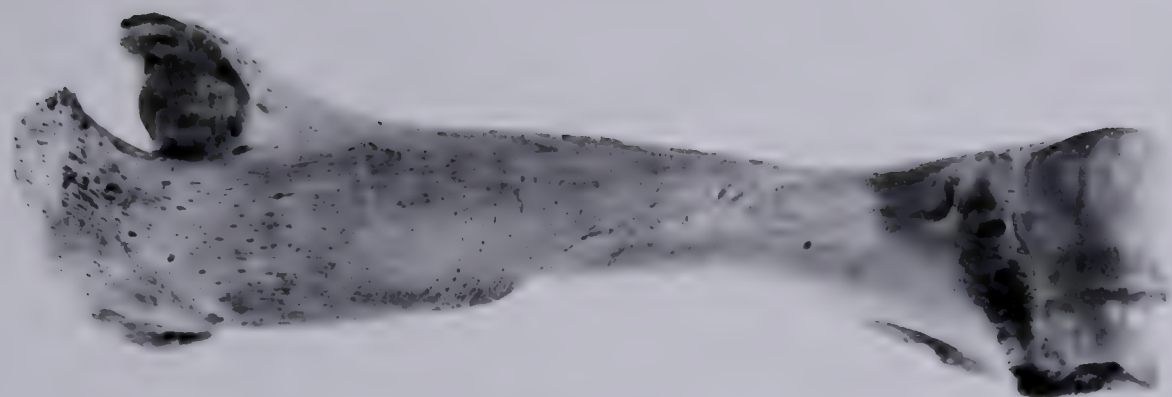
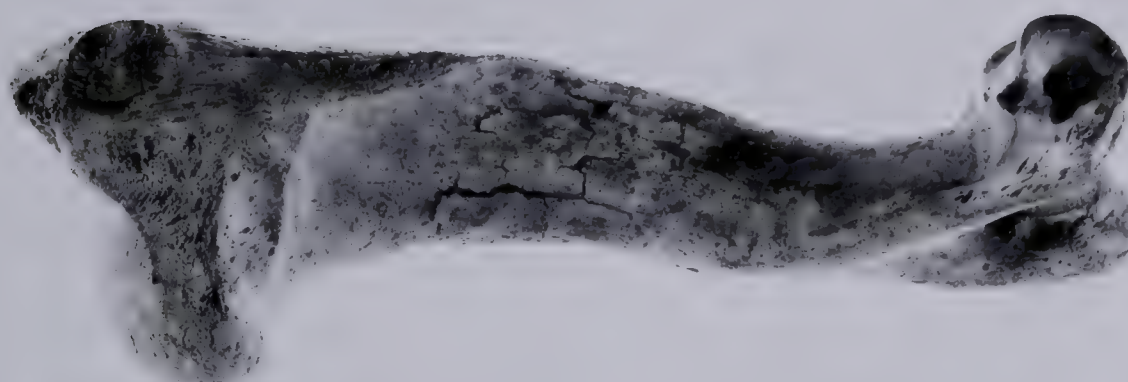
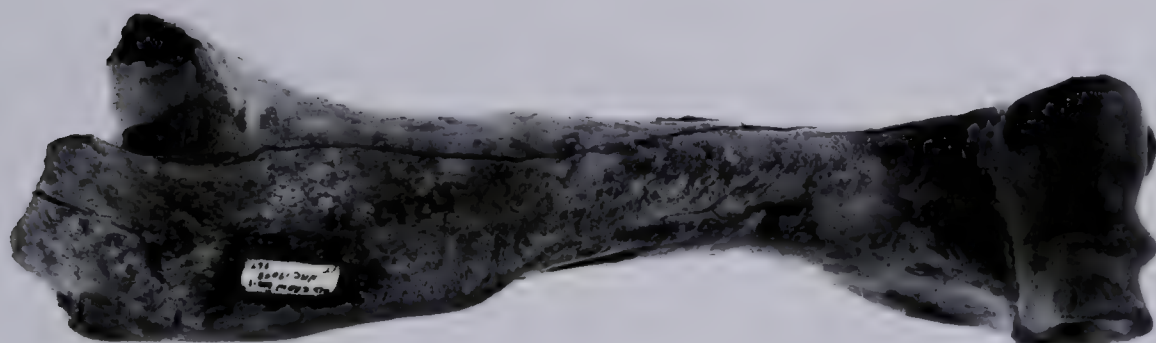


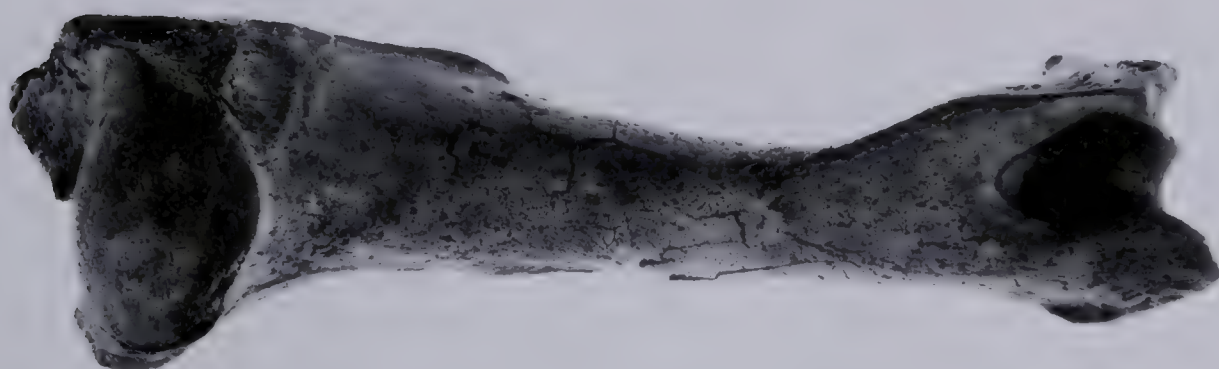
Figure 68. A. Anterior views of a right humerus (NMC 17048, Old Crow Locality 1) of a postglacial wapiti (*Cervus elaphus*) (left) and a right humerus (NMC 36163, Alberta) of a Recent wapiti (*Cervus elaphus*) (right). B. Lateral view of NMC 17048. Note large facets on the lateral epicondyle (bottom centre) and the posterior lateral tuberosity (top centre). C. Posterior views of NMC 17048 (right) and NMC 36163. Note facet on bottom right of NMC 17048, which yielded a radiocarbon date of $4,570 \pm 100$ years B.P. (I-7796).



A
5 CM



B
5 CM



C
5 CM

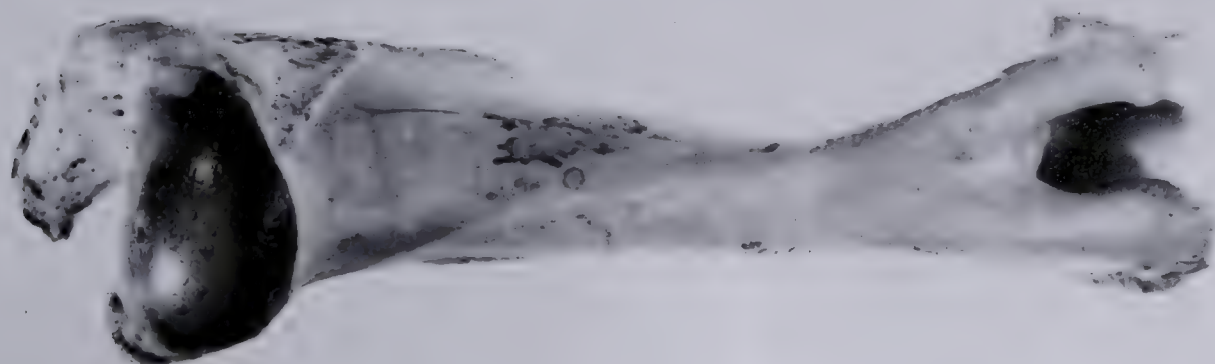


Table 74. Measurements of Pleistocene wapiti (*Cervus elaphus*) antlers from the Yukon Territory and Alaska compared to a Recent wapiti antler from Alberta.

Specimens	Measurements (mm)*				
	1	2	3	4	5
<i>Cervus elephus</i> .Pleistocene, Y.T.					
DCMP-3 Sulphur Creek (Dawson Area)	110.0	90.0	1180.0	910.0	195.0
NMC 11672 Dawson Loc. 15	73.0 [†]	65.5 [†]	-	-	170.0
<i>Cervus elaphus</i> .Pleistocene, Alaska					
NMC 25873 Lost Chicken Creek	99.0	88.0	-	-	179.0
<i>Cervus elaphus</i> .Recent, Alberta					
NMC 11691 Waterton	91.3	81.5	1120.0	710.0	160.0

*1 - Maximum diameter of antler base.

2 - Minimum diameter of antler base.

3 - Straight line measurement from base to tip of most distal tine.

4 - Length along beam from antler base to main distal fork (fork between fifth and sixth tines in DCMP-3).

5 - Circumference of beam midway between base and main distal fork.

Table 75. Measurements of a Pleistocene wapiti (*Cervus elaphus*)
cranial fragment from the Yukon Territory compared to
crania of Recent wapiti from Alberta.

Specimens	Measurements (mm)*			
	1	2	3	4
<i>Cervus elaphus</i> .Pleistocene, Y.T.				
NMC 6750 Dawson Loc. 5	66.8	117.4	61.8	56.0
<i>Cervus elaphus</i> .Recent, Alberta				
NMC 36163 Banff	59.3	111.3	55.8	53.9
NMC 11691 Waterton	44.0a	112.1	62.3**	61.3**

*1 - Distance between the fronto-parietal and occipital sutures on the mid-line.

2 - Minimum cranial breadth immediately posterior to the antler pedicels.

3 - Maximum diameter of antler pedicel.

4 - Minimum diameter of antler pedicel.

** Antlers attached.

Table 76. Measurements of a postglacial wapiti (*Cervus elaphus*) humerus from the Yukon Territory compared to humeri of Recent wapiti from Alberta.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Cervus elaphus</i> . Postglacial, Y.T.							
NMC 17048 Old Crow Loc. 1	334.0 [†]	96.0	302.0	37.0	47.0	73.0	72.0
<i>Cervus elaphus</i> . Recent, Alberta							
NMC 36163 Banff	332.0	101.0	299.0	34.0	45.0	73.0	72.0
NMC 33481 -	336.0	102.0	301.0	36.0	46.0	74.0	72.0

*1 - Total length.

2 - Maximum proximal depth.

3 - Proximal end of head to distal end of lateral condyle.

4 - Minimum width of shaft.

5 - Minimum depth of shaft.

6 - Maximum distal width.

7 - Maximum distal depth.

antlers is the presence of a well developed supernumerary tine above the first (brow) and second (bez) tines. Although Murie (1957) has not recorded supernumerary tines of this type in Recent North American wapiti, they are known from Europe (Winans 1913). Some measurements of DCMP-3 are recorded in Table 74.

NMC 11672 from Dawson Locality 15 is the proximal third of a shed right antler. It retains traces of the deep, longitudinal vascular grooving that helps to distinguish *Cervus* from *Rangifer* antlers. The first and second tines are broken near their roots. Only minimum measurements (Table 74) can be recorded on the antler base because it is heavily eroded.

The tips of two antlers (NMC 17259, 11710) from Dawson Locality 28 are referred to *Cervus elaphus* because of their ridged and knobby surface and roundness, which characterize the appearance of Recent wapiti tines examined. The tip of NMC 11710 has been gnawed by a rodent.

A heavily eroded dorsal fragment of a cranium with antler pedicels (NMC 6750) from claim 19 on Eldorado Creek (near Dawson Locality 5) is of historic as well as paleontological interest, for it was collected by the surveyor William Ogilvie in 1898. It was recovered at a

depth of 19 feet (5.8 m) below the surface. Although a note with the fossil indicates that it was derived from Klondike gravels, matrix still adhering to it consists of fine micaceous silt or muck. The presence of antler pedicels and the degree of suture fusion indicate that a male in early maturity is represented. All morphological features preserved on NMC 6750 are readily matched in a Recent male wapiti cranium (NMC 36163). The antlers had been shed before death, because only the pedicels are present. Stags usually begin to drop their antlers in February and start growing them again in April (Banfield 1974, p. 399), so the individual represented by the fossil probably died between February and April. Some measurements are provided in Table 75. Fine rootlet impressions are seen on the upper surface of the fossil, suggesting burial in a grassland environment.

NMC 17048 from Old Crow Locality 1 is a nearly complete right humerus. It is well preserved (even to detailed surface sculpture), relatively pale (more like the 12,000-year-old bones from Old Crow Locality 11(1) than the older, darker bones from the Old Crow Basin), and matches very closely two Recent adult wapiti humeri (NMC 33481, 36163).

Facets are evident on NMC 17048, being most easily seen on the lateral epicondyle and on the posterior prominence of the lateral tuberosity near the head of

the humerus. The alignment of small parallel grooves on these facets suggests that the bone was ground down at an angle not quite perpendicular to its long axis. The camber and high polish on the facets, most noticeable near their margins, suggest that the humerus was later rubbed across a soft surface. Facets on this bone are reminiscent of those discovered on other more deeply stained, and almost certainly, much older bones from the Old Crow Basin. While most of the specimen has been sacrificed to obtain a radiocarbon date, the parts showing the clearest facets have been preserved in case archeologists are interested in trying to establish whether they have been made by man or other natural causes. Radiocarbon analysis of the shaft of this specimen yielded a date of $4,570 \pm 100$ years B.P. (I-4225), indicating that wapiti lived in the Old Crow Basin during postglacial time.

Discussion

Except for NMC 11672, which is heavily eroded, Yukon Pleistocene wapiti seem to have been slightly larger than modern Alberta wapiti, according to comparisons of various skeletal elements. Probably most wapiti specimens from the Dawson Area are of late Wisconsin age, for they are not deeply stained. The single specimen from the Old Crow Basin evidently represents an animal that lived

there about 4,600 years ago. Wapiti no longer occur in Alaska or the Yukon, so they may have become extinct in Eastern Beringia, or they may have withdrawn southward, during the hypsithermal.

In other parts of Canada, wapiti remains varying in age from Pleistocene to Recent have been reported from Ontario (e.g. Hamilton (Burlington Heights) - late Wisconsin to postglacial; Strathroy - postglacial to Recent?; Kingston - postglacial to Recent?; Waterford - postglacial to Recent (antler in Eva Brook Donly Museum, Simcoe), Sydenham - postglacial to Recent?; Lanark - postglacial to Recent?), Saskatchewan (e.g. Saskatoon - Sangamon interglacial or mid-Wisconsin; Veregin - Pleistocene to Recent; Oxbow - postglacial (approximately 5,000 years old)), Alberta (e.g. Edmonton - late Pleistocene; Medicine Hat - Sangamon interglacial), British Columbia (e.g. Hanging Valley Creek - postglacial to Recent?; Australian - postglacial?; Kamloops area - postglacial to Recent?), and the Northwest Territories (Julian archeological site at Fisherman Lake) (Hay 1923, Cowan 1941, Stalker and Churcher 1970, Harington 1976 MS., Fedichichuk 1970, and records and specimens in the Quaternary Zoology Section, National Museums of Canada). According to this evidence, the earliest recorded wapiti from Canada are of Sangamon interglacial age, and wapiti became most

widespread and abundant in southern Canada during the postglacial.

In the conterminous United States, wapiti remains are widespread, but mainly northern. The earliest reports from Cumberland Cave, Maryland (Kansan) and Conard Fissure, Arkansas (early Illinoian), require further substantiation. *Cervus elaphus* bones have been recorded from Wisconsin and postglacial sites in Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Michigan, Minnesota, Missouri, New Jersey, New York, North Carolina, Oklahoma, Pennsylvania, Tennessee, Vermont, Virginia, Washington, Wisconsin and Wyoming (B. Kurtén, personal communication 1976).

Many specimens referred to *Cervus elaphus* have been collected from Alaska. Most are from Wisconsin sediments (but a few appear to be of Illinoian age (Guthrie and Matthews 1971, p. 496)) at the following localities near Fairbanks: Cripple Creek, Fairbanks Creek, Gold Hill, Engineer Creek, Lower Goldstream Creek, and Dome Creek. Other specimens have been collected at Chicken, Ingle and Lost Chicken creeks in eastern Alaska; Gertrude Creek in central Alaska; and Rainbow Mine and Koyuk River in western Alaska. The localities span the Eastern Beringian

refugium (Guthrie 1966, Figure 1, Table 1).

Measurements of a shed left antler (NMC 25873) from Lost Chicken Creek are given in Table 74. There is no proximal supernumerary tine. The distal halves of first, second and third tines are lacking, and the main beam is broken just beyond the root of the third tine. NMC 25873 is light in color, and is probably of late Wisconsin age.

The earliest record of *Cervus* cf. *elaphus* in North America and Beringia is based on a P⁴ and a naviculocuboid from ?Nebraskan deposits at Cape Deceit (Guthrie and Matthews 1971, Figure 10).

The only record of *Cervus elaphus* in the major Pleistocene mammal faunas of Siberia is from the early Wisconsin Iedoma Suite in the Kolyma Lowland (Sher 1971).

In Europe, *Cervus elaphus* of the acornate type (often having five tines including a simple terminal fork; Kahlke 1959, Figure 5; Kurtén 1968, Figure 69) has been recorded from Günz (?Nebraskan) deposits at Süssenborn and Mindel (?Kansan) deposits at Mosbach in Germany. Coronate forms occurred as early as the Günz at Hundsheim, and by Cromerian (?Aftonian) interglacial time, red deer of the modern type had spread through central Europe. Kurtén (1968, p. 162) remarks that the European fossil record shows that

the simpler acornate form became dominant during cold phases, and the coronate forms held sway during the warmer phases of the Pleistocene. Perhaps largest and most complex antlers are developed by wapiti and red deer during periods when nutritive conditions in the environment are most favorable for this species. *Cervus elaphus* was common in Europe during the late Pleistocene.

Dietrich (1938) suggests that the simpler acornate form of *Cervus elaphus* evolved from an early Villafranchian species with three or four tines on each antler, *Metacervocerus pardinensis*, which is known from Perrier. So *Cervus elaphus* seems to have originated in Europe about the beginning of the Pleistocene. During the early Pleistocene (Günz - Nebraskan), favorable environmental conditions seem to have resulted in a radiation of *Cervus elaphus* from Europe to Alaska. Wapiti may have penetrated southern North America by Kansan (Cumberland Cave) or early Illinoian (Conard Fissure) time, but those records must be better substantiated. Firmer evidence (Medicine Hat) indicates that wapiti were present on the southwestern prairies during the Sangamon interglacial, and that they occupied the Eastern Beringian and southern refugia during the Wisconsin glaciation. During the postglacial they became extinct in or withdrew from Alaska and the Yukon, and became abundant and widespread throughout central North America. Since the European

occupation of North America, wapiti herds have been greatly decimated, becoming extinct in most parts of their range except the western mountain regions and relatively isolated hilly areas.

Wapiti or red deer (*Cervus elaphus*) are Holarctic in distribution, having occupied Scotland, continental Europe, central Asia, and northern North America in early historic time. Wapiti are large, sturdy deer. Males average 7.5 feet (231 cm) in length and 700 pounds (315 kg) in weight. They have prominent white rump patches, and males carry long curving antlers with many tines. During the summer, they travel in bands. Females and calves, often numbering about 25, forage together, while males form bachelor bands. Large herds of 100 or more animals form after the rut. They are a migratory species, at least in the mountainous areas, where winters are spent in protected valleys and summers are spent in high alpine valleys.

Wapiti prefer open areas, such as alpine pastures, marshy meadows, prairies and aspen parkland. In Eastern Beringia during the Pleistocene they seem to have thrived in cool, dry grassland or open parkland conditions. The species feeds mainly on willow, aspen and poplar twigs and leaves, bark, herbs and grasses. Apart from man, the main predators of the wapiti are the mountain lion, wolf and brown bear.

All of those predators lived in the Yukon during the Pleistocene.

Alces latifrons (giant moose)

Antler beams of giant moose (Figures 69A-C, 70, Table 77) are not uncommon in Yukon Pleistocene deposits. All but two of those reported are from the Old Crow Basin. Antler beams of this species have been described previously from Alaska under the name "*Cervalces alaskensis*" (Frick 1937, p. 203), but there is no doubt that they are very different in size and proportion to beams of the best preserved specimen (PU 10648) of *Cervalces scotti* (Scott 1885, p. 191, Figure 5), while they conform closely to antler beams of Eurasian *Alces latifrons*.

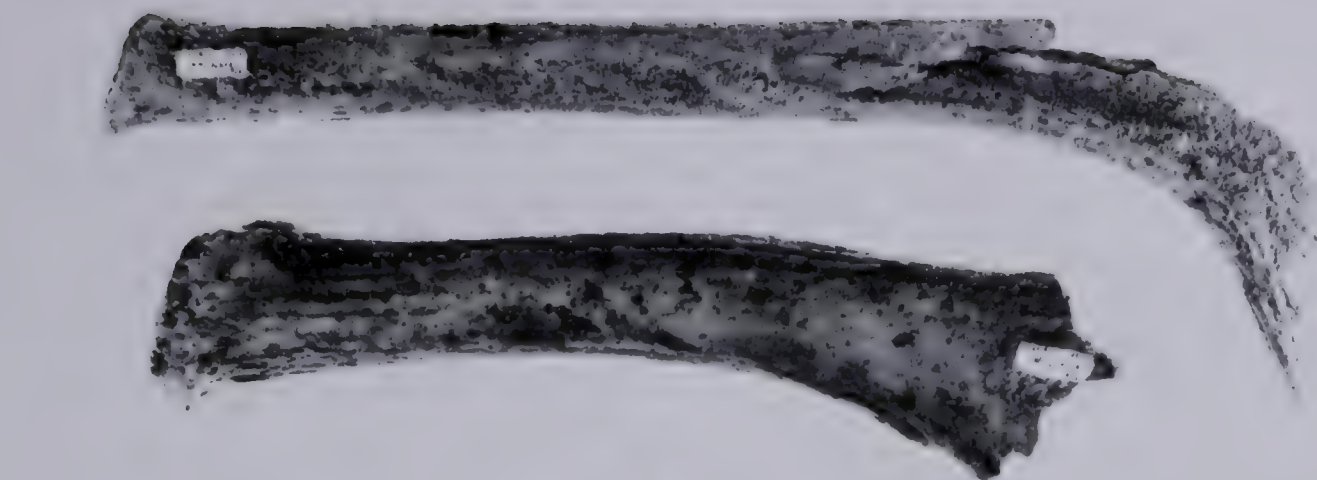
I was first convinced that *Alces latifrons* was represented in Eastern Beringian ice age deposits in 1966 when attempting to identify a massive antler beam (NMC 10477) collected by V. Rampton in 1962 on the Old Crow River. Fossils collected since then have reinforced the preliminary evidence, and I suggest that many specimens previously described as *Cervalces* (e.g. *C. roosevelti*, *C. borealis*) actually represent *Alces latifrons*, and indicate that this giant moose had reached southern North America from Eastern Beringia by at least Sangamon time and perhaps as early as Kansan time.



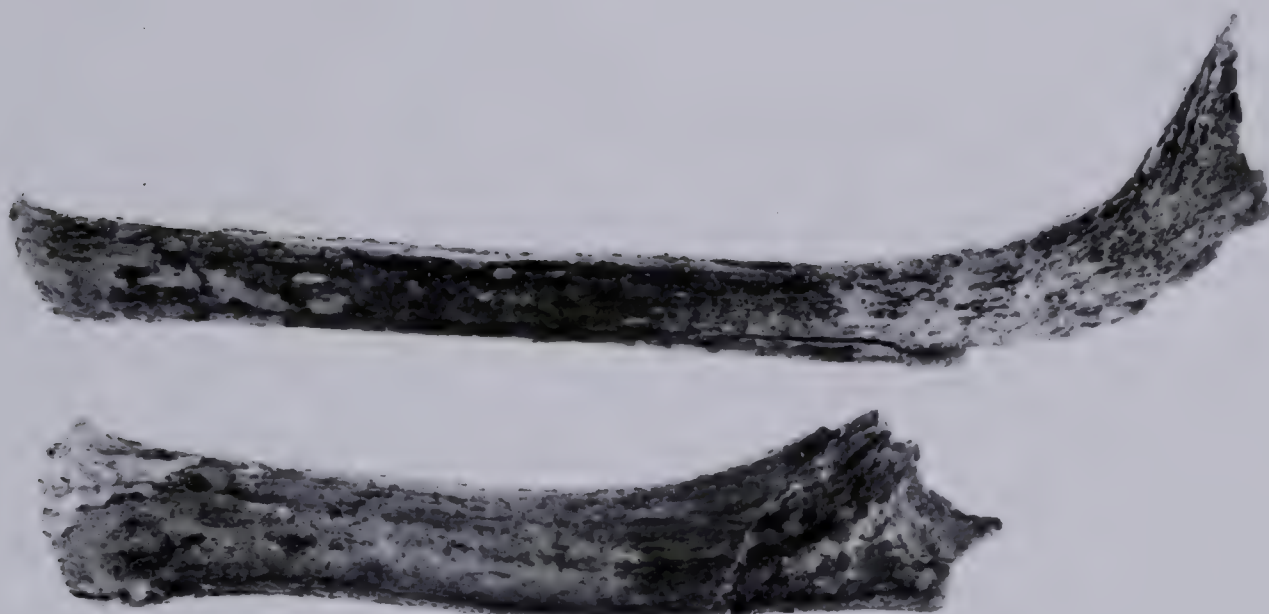
Figure 69. A. Dorsal views of a left antler beam (NMC 16505, Old Crow Locality 8) of a Pleistocene giant moose (*Alces latifrons*) (top) and a left antler beam (NMC 15258, Old Crow Locality 22) of a Pleistocene giant moose (*Alces latifrons*) (bottom).

B. Anterior views of NMC 16505 (top) and NMC 15258 (bottom).

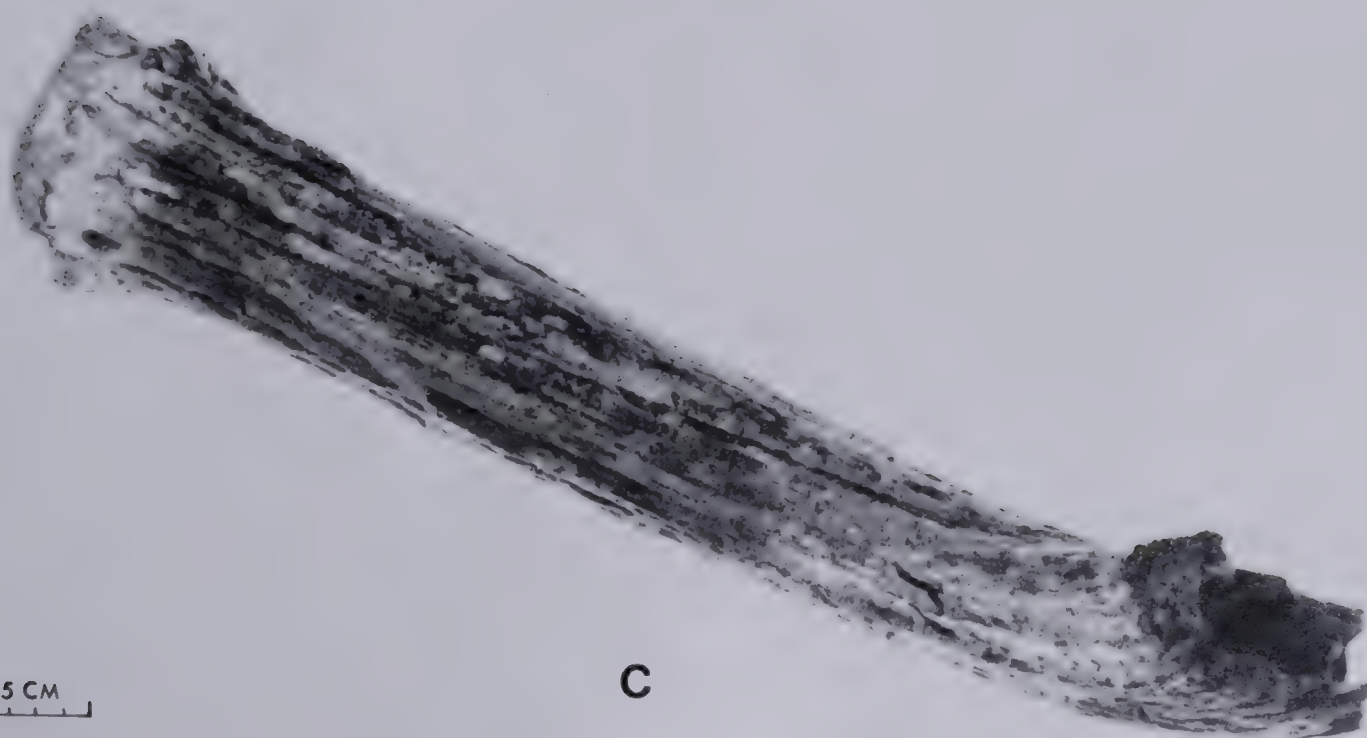
C. Anterior view of a left antler beam (NMC 10477, Old Crow Locality 8) of a Pleistocene giant moose (*Alces latifrons*).



5 CM

A

5 CM

B

5 CM

C



Figure 70. Restoration of a giant moose (*Alces latifrons*) charging wolves (*Canis lupus*).
Ink sketch by Bonnie Dalzell.



Table 77. Measurements of Pleistocene giant moose (*Alces latifrons*) antlers from the Yukon Territory and Alaska compared to those of *Alces latifrons* from Eurasia and *Cervalces scotti* from the United States.

Specimens	Measurements (mm)*								
	1	2	3	4	5	6	7	8	9
<i>Alces latifrons</i> . Pleistocene, Y.T.									
NMC 16505 Old Crow Loc. 8	460	61	55	155	46	42	44	39	296.8
NMC 10477 Old Crow Loc. 8	430	110	75	290e	74	73	71	69	148.3
NMC uncatalogued Old Crow Loc. 22	397 [†]	82	76	230	61	61	61	60	-
NMC 25969 Dawson Loc. 29	386	75	58	195	60	54	57	53	194.9
NMC 24150 Old Crow Loc. 11S	365 [†]	75	70	200	59	55	55	50	-
NMC 15258 Old Crow Loc. 22	350a	77	67	204	58	54	53	50	171.6
NMC 11336 Dawson Loc. 25	320	71	65e	160	47	46	45	40e	177.8
NMC 13616 Old Crow Loc. 11A	300e	88	67	200	55	48	-	-	170.0
NMC 13615 Old Crow Loc. 11A	-	85	73	230	67	56	68	57	-
NMC 27113 Old Crow Loc. 2 ^o (immature?)	196 [†]	34	30	98	26	24	29	28	-
							Average		159.9
<i>Alces latifrons</i> . Pleistocene, Alaska Fairbanks area (Khan 1970, p. 55)									
F:AM 30497	450	-	-	-	70a	-	70a	-	-
F:AM 30496	430	-	-	-	60a	-	60a	-	-
F:AM field no. 3858	290	-	-	-	75a	-	75a	-	-
<i>Alces latifrons</i> . Pleistocene, Siberia**									
GIN <u>835-525</u> 32 Bolshaya Chukochya	500e	86	63	233	83	69	59e	60e	216.6
Catalog no. unknown Khara-aidan	496	114	110	237	86	85	-	-	172.2
GIN 361 Aldan	400	115	97	260	89	60	-	-	184.8
GIN "873" Kolyma Lowland	307	89	59	185	-	-	-	-	165.1
GIN 426 Yenesei	300	130	97	240	83	66	-	-	122.5
							Average		163.8
<i>Alces latifrons</i> . Pleistocene, Europe Mosbach, Germany (Sher 1971, Table 27)									
M	382	89	89	223	68	67	-	-	171.2
OR	240-	73-	71-	186-	51-	57-	-	-	135.3-
	500	114	113	270	87	83	-	-	185.2
N	25	16	16	73	19	19	-	-	23
<i>Cervalces scotti</i> . Pleistocene, U.S.A.***									
Catalog no. unknown, Topeka, Kansas	220	72	-	-	-	-	58	50	-
Uncataloged, Columbia, New Jersey	215	98	90a	210	62	55	50	52	102.4
Catalog no. unknown, Mount Herman, New Jersey	185	91	81	-	55	53	53	52	-

* 1 - Length of beam from burr to beginning of palmation.

2 - Maximum diameter of burr.

3 - Minimum diameter of burr.

4 - Circumference of beam directly distal to burr.

5 - Maximum diameter of beam (50 mm from burr).

6 - Minimum diameter of beam (50 mm from burr).

7 - Maximum diameter of beam (100 mm from burr).

8 - Minimum diameter of beam (100 mm from burr).

9 - Slenderness index (SI) $\frac{\text{Measurement 1}}{\text{Measurement 4}} \times 100$.

Slenderness is directly proportional to the loading.

** I am grateful to A.V. Sher for allowing me to measure specimen GIN 835-525 and GIN "873" during a visit to the Paleontological Institute, USSR Academy of Sciences, Moscow. Measurements of the remaining specimens are derived from Table 27 (Sher 1971).

*** I am grateful to G.L. Sawyer for allowing me to measure the Columbia specimen and to C.S. Churcher for data on the Mount Herman and Topeka specimens.

I follow Kahlke (1956, Vol. II, p. 12) in considering *Alces* the most appropriate generic designation for the giant moose rather than *Libralces* (Azzaroli 1953, pp. 16, 19). In this respect, I agree fundamentally with the opinions expressed by Sher (1971, p. 196).

Referred specimens

The largest antler beam recovered so far from deposits in the Yukon Territory is NMC 10477 from Old Crow Locality 8. It is darkly stained and closely matches antler beams from near Fairbanks, Alaska (particularly F:AM 30496) and the Aldan River in Siberia (GIN 361). It is larger than the holotype of *Alces latifrons* from Norfolk, England described by Johnson (1874, p. 1), which has a beam measuring approximately 300 mm from burr to beginning of palmation, and a beam diameter of approximately 63 mm. NMC 10477 is displayed in the National Museum of Natural Sciences, Ottawa.

NMC 24150 from Old Crow Locality 11S is part of a right antler beam. There is no indication of the beginning of the palmation at the distal end, so probably it was relatively long. The surface of this specimen has been heavily eroded, as have the others. A few show evidence of very deep, longitudinal vascular grooves,

however. NMC 15258 from Old Crow Locality 22 is a right antler beam. Only a few patches of the original surface are preserved near the burr. Its ventral surface extends farther into the palmation than does the dorsal surface. NMC 16505 from Old Crow Locality 8 is a right antler, which, although longer (460 mm) from burr to beginning of the palmation than any other giant moose antlers collected from the Yukon, is unusually gracile. This is indicated by its very high slenderness index (Table 77). Perhaps its slenderness can be explained by the lack of full maturity of the individual that bore it. NMC 25969 from Dawson Locality 29 is a right antler beam, the dorsal surface of which extends well into the palmation. Its surface has been heavily eroded. The specimen is paler than any of the Old Crow specimens, which are stained dark brown. NMC 27113 from Old Crow Locality 29 is a small, right antler beam. Because of the similarity of its proportions to beams from mature males of *Alces latifrons*, it is tentatively considered to represent an immature giant moose.

NMC 11336, a left antler fragment from Dawson Locality 29, is unique among the Yukon specimens in that the first posterior tine is largely preserved (perhaps the distal quarter is missing). In that feature it

matches a well preserved left antler of *Alces latifrons* from middle Pleistocene gravels from Süssenborn, Germany (Kahlke 1956, Vol. I, Plate 2), and is radically different from the condition at the beginning of the palmation in a recently discovered specimen of *Cervalces scotti* from Columbia, New Jersey (in the personal collection of G.J. Sawyer, Paulina, New Jersey), with which it was directly compared. Relative to the Yukon giant moose specimens, *Cervalces scotti* has much shorter antler beams (averaging approximately 207 mm - less than 55% of the Yukon *A. latifrons* average), and the anterior and posterior parts of the palmation rise sharply upward, almost simultaneously, whereas in *Alces latifrons* the part of the antler at the beginning of the palmation lies nearly flat, and the posterior segment of the palmation begins its backward curve much closer to the burr than the anterior segment.

NMC 13618 from Old Crow Locality 11A is a left antler beam lacking the distal half of the dorsal surface. The outer surface is blackish brown, while the exposed inner antler material is paler and shows evidence of replacement by iron oxide. NMC 13615 from Old Crow Locality 11A is the medial 214 mm of a left antler beam. It is heavily eroded and iron-stained. The robustness of the beam suggests that, in its original

condition, it may have approached NMC 10477 in size. An uncataloged antler beam from Old Crow Locality 22 was equally large. Most of it was sacrificed to obtain a radiocarbon date.

The following basal fragments, probably representing originally long antler beams, are referred to *Alces latifrons*: NMC 14908 from Old Crow Locality 31; NMC 14056 from Old Crow Locality 8; and NMC 16378 from Old Crow Locality 67.

Discussion

The Yukon giant moose specimens are considered to be mainly of pre- late Wisconsin age. Probably none of the specimens is older than those from the Olyor Suite (?Kansan) in the Kolyma Lowland of Siberia. If the radiocarbon date on an uncataloged antler beam from Old Crow Locality 22 is correct ($33,800 \pm 2,000$ years B.P. (I-4229)), then giant moose may have survived until mid - Wisconsin time in Eastern Beringia. Generally, the Yukon antler beams are more slender than those of Eurasian *Alces latifrons* (Table 77).

In other parts of Canada, long, massive moose-like antler beams are known from deposits of probable Sangamon interglacial age at Fort Qu'Appelle, Saskatchewan, and

from Sangamon or early Wisconsin sediments at Toronto, Ontario. I tentatively refer the former (NMC 11961 - 310 mm long from burr to palmation, with a beam diameter of 50 mm), designated as *Cervalces roosevelti* by Khan (1970, p. 55, Figure 2), and more doubtfully the latter (ROM 20176 - 330 mm long from burr to palmation, with a beam diameter of 60 mm), designated as *Cervalces borealis* by Bensley (1913, p. 2), to *Alces latifrons*. An unusual feature of ROM 20176 is the pronounced upward convexity of the beam. It is worth noting that a moose-like deer ("*Alces* sp.") has been reported from Sangamon interglacial deposits at Medicine Hat, Alberta (Stalker and Churcher 1970).

Perhaps some of the larger antler beams referred to *Cervalces roosevelti* from the conterminous United States (e.g. Denison, Iowa (Hay 1914, pp. 261-269); Giltner, Nebraska (Cook 1931, p. 279)) represent the giant moose *Alces latifrons*. The Giltner specimen is considered to be of Kansan age.

At least two antler beams (F:AM 30496, 30497), and possibly a third (F:AM field no. 3858), from ice age sediments in the Fairbanks area of Alaska are referred to *Alces latifrons*. Although designated

"*Cervalces alaskensis*" by Frick (1937, p. 203), there is no doubt that they are closer to the type of *Alces latifrons* than the most complete specimen (PU 10648) of *Cervalces scotti*, a fact suspected by Sher (1971, p. 199).

In Siberia, *Alces latifrons* is recorded from the Olyor Suite (?Kansan) on the Bolshaya Chukochya River (Sher 1971, Plate XIV-4), and from other sites containing fossils of possible middle Pleistocene age (e.g. Aldan, Yenesei, Lena (Vangengeim 1961), and Khara - Aldan (Rusanov 1968)). It is also known from western Siberia (Vangengeim and Zazhigin 1965). *Alces latifrons postremus*, with antlers approaching those of the modern moose, *Alces alces*, has been described by Vangengeim and Flerov (1965). It has been reported from Mindel - Riss (?Kansan - Illinoian) deposits in Yakutia and Kamchatka (Sher 1971, Table 27). Possibly this form lies closer to *Alces alces* than to *Alces latifrons* (Sher 1971, p. 197).

In other parts of the Soviet Union, the giant moose is known from the Urals (Yakhimovich 1965) and Kazakhstan (Bazhanov and Kostenko 1962). It is also an important member of the Tiraspol faunistic complex (Gromov 1948), which is typical of the Mindel (?Kansan) of the southern area of the European part of the Soviet

Union. Tiraspol in Moldavia is the most important locality for middle Pleistocene biostratigraphic correlation between Europe and Asia (Kahlke 1973, p. 24).

In Europe, *Alces latifrons* had become well established during the Cromer (?Aftonian) interglacial and Mindel (?Kansan) glacial phases (e.g. Cromer Forest Bed, Norfolk, England; Mauer, Mosbach, Süssenborn, Germany).

The earliest stages of moose evolution are poorly known. In Vereshchagin's (1967b, Figure 6) phylogeny of the Tribe Alcini, *Alces latifrons* is derived from a *Eucladoceros* stock in the latter half of the late Pliocene. He considers *Cervalces scotti* and *Alces alces* to be early Pleistocene offshoots from *Alces latifrons*. Kurtén (1968, p. 167) believes the earliest recognizable ancestor of the moose to be the Gallic moose (*Alces gallicus*) of the Villafranchian of Europe (e.g. the Craggs in Norfolk; Senèze and possibly Perrier in France; and Erpfingen in Germany). A large antler beam from deposits near Kumertau in the southern Urals, considered by Vereshchagin (1967, p. 9) to be of late Pliocene age, may be referable to this taxon. The Gallic moose was about the same size as

Alces alces, but its antlers were shaped like long-handled spoons. The small palmation was fringed with short tines. Its antlers had a span of 3 m or more, suggesting that it could not have lived in heavily forested regions.

The transition from the Gallic moose to the giant moose evidently occurred near the earliest part of the middle Pleistocene in Europe (e.g. Mosbach I, Germany, and the Waalian (?Nebraskan) interstadial of the Forest Bed in Norfolk, England). The antler palmations of the moose at this stage were smaller, and the beams were longer than those typical of later *Alces latifrons* (Kurtén 1968, p. 168). During the Mindel (?Kansan), there was a remarkably broad dispersal of giant moose from England, through Germany, Moldavia and Siberia to Alaska and the Yukon, and possibly to southern North America (Giltner, Nebraska). Presumably this dispersal was concomitant with the spread of cool, grasslands and parklands in the northern Holarctic region. Evidently *Alces latifrons* gave way to *Alces alces* in Siberia during the Mindel - Riss (?Kansan - Illinoian) period. The giant moose seems to have been present as late as Sangamon (Fort Qu'Appelle) or possibly Wisconsin time in southern North America, while it evidently survived

until mid-Wisconsin time in Eastern Beringia.

I think that the fossil evidence indicates a general reduction in beam length and an increase in palmation area from late Pliocene to Recent. All stages seem to be present, e.g. *Alces gallicus* - *Alces latifrons* - *Alces latifrons postremus* - *Alces alces*. This reduction of beam length and increase in palmation area suggests an increasing use of boreal forest habitat throughout the Pleistocene. Such a trend may have been induced by growing competition with more specialized cool grassland or parkland herbivores like mammoths, muskoxen, wapiti or red deer, and bison. Therefore, I cannot agree with Vereshchagin's (1967, p. 10) statement that "It is difficult to concede the possibility that the highly specialized, long-beamed antlers of *Alces latifrons* were transformed during the first half of the Pleistocene into the short-beamed antlers of the present-day elk {moose}".

Alces latifrons seems to have had as broad a range in the middle to late Pleistocene of the Holarctic as the woolly mammoth had in the late Pleistocene. The giant moose stood 1.9 to 2 m at the shoulders (Kurtén 1968, p. 168) and was characterized by antler beams 300 to 500 mm in length, with an equal length being given to the palmation. Its skull was heavily built and its limbs were much stouter and longer

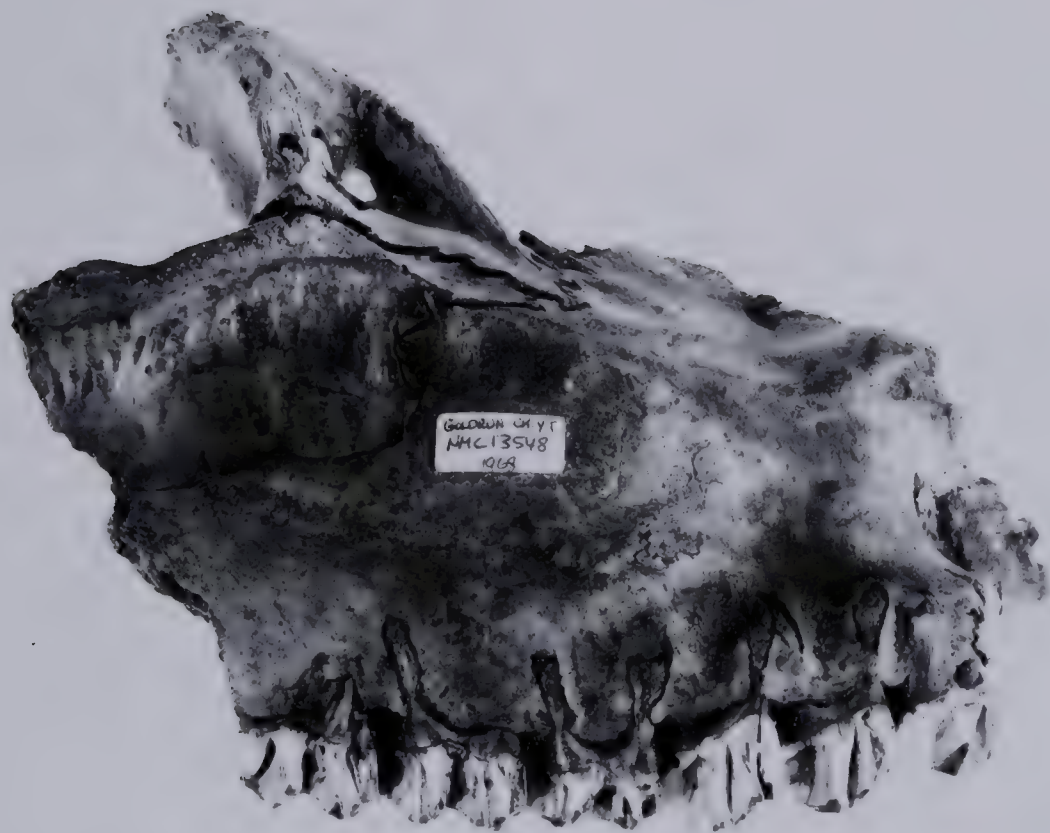
than those of the modern moose (Sher 1971, Plate XIV-1, 2). Like its ancestor the Gallic moose, the giant moose was not adapted to dense forest. In addition to the great span of the antlers that would hamper movement of the giant moose in heavily forested areas, paleobotanical data from Tiraspol indicate that *Alces latifrons* occupied cool forest-steppe or parkland regions away from dense forest. Probably cool, tundra-like grasslands with steppe elements were predominant in the Kolyma and Aldan regions when *Alces latifrons* lived there (Sher 1971, p. 198, Giterman 1973, p. 67). Therefore, I suggest that the giant moose is a paleoenvironmental indicator of cool steppe-like grasslands or parklands. Nothing is known of the feeding habits of this species - presumably marsh plants, willows and other shrubs were important dietary items. Probably wolves were among its major predators.

Alces alces (moose)

Moose remains (Figures 71A-B, 72A, Tables 78-80) are fairly common in Pleistocene deposits. Except for a few cranial and postcranial specimens from Gold Run Creek that are relatively complete and are clearly assignable to *Alces alces*, only readily identifiable antler fragments are described. A description of other skeletal material will be deferred until casts of *Alces latifrons* are available to



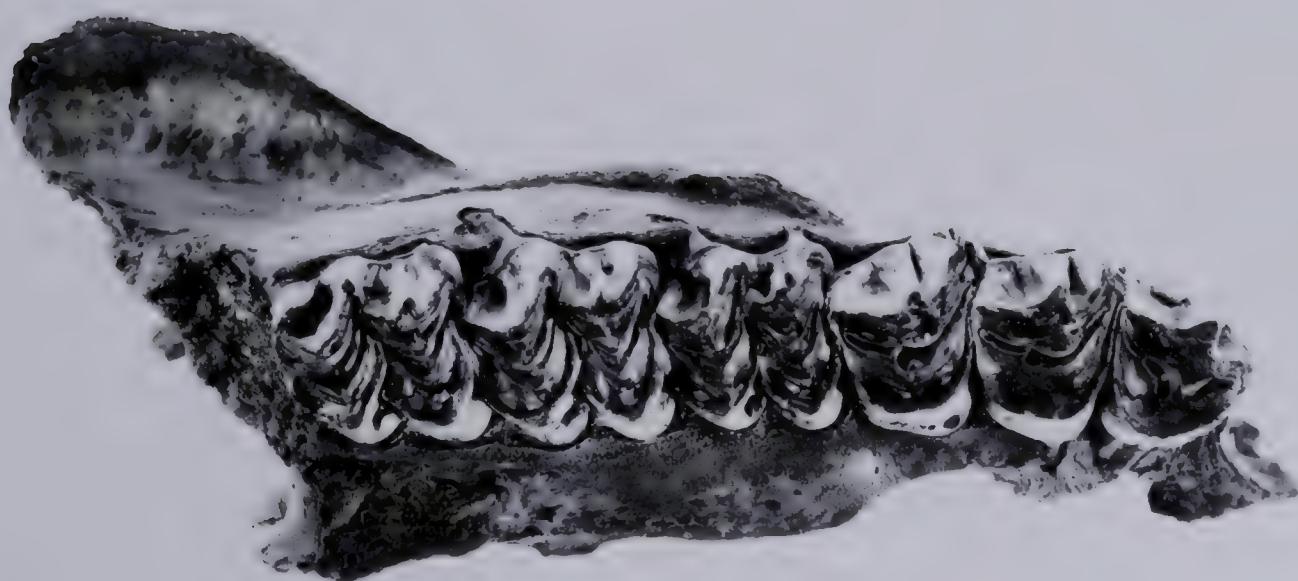
Figure 71. Right facial fragment with RP^2-RM^3
(NMC 13548, Dawson Locality 32) of a
Pleistocene moose (*Alces alces*).
A. Lateral view.
B. Occlusal view.



5 CM

A

5 CM



B

Table 78. Measurements of Pleistocene moose (*Alces alces*) antlers from the Yukon Territory compared to those of Recent moose from Ontario.

Specimens	Measurements (mm)*								
	1	2	3	4	5	6	7	8	9
<i>Alces alces</i> , Pleistocene, Y.T.									
NMC 29003 Dawson Loc. 17	210	72	53	184	60	47	57	46	114.1
NMC 10474 Dawson Loc. 19	200	106	74	195	59	54	56	51	102.6
NMC 10473 Dawson Loc. 19	190	91	76	190	59	51	60	51	100.0
NMC 25197 Old Crow Loc. 19	190	73	65	170	46	45	50	41	111.8
NMC 29004 Dawson Loc. 17	180	84	77	217	64	56	62	53	83.0
NMC 29002 Dawson Loc. 17	180e	77	72	184	52	46	53	46	97.8
NMC 14006 Old Crow Loc. 1	180	83	67	174	51	44	46	43	103.5
NMC 28527 Old Crow Loc. 143	175	89	73	215	66	57	58	56	81.4
NMC 11667 Dawson Loc. 13	175	71	62	185	53	48	56	43	94.6
NMC 16255 Old Crow Loc. 18	170	86	72	200	53	51	60	43	85.0
NMC 17512 Dawson Loc. 32	165	78	68	185	53	49	56	43	89.2
NMC 13547 Dawson Loc. 32	160	82	75	200	62	53	71	47	80.0
NMC 29232 Dawson Loc. 13	160	61	52	174	48	45	50	39	92.0
NMC 27082 Old Crow Loc. 32E (immature?)	160	58	41	110	39	35	47	29	105.7
NMC 17559 Dawson Loc. 32	150	69	63	177	46	44	56	40	84.8
NMC 16929 Porcupine R. (Johnson Village)	145	58	52	161	47	43	57	39	90.1
NMC 26923 Old Crow Loc. 21	142	71	57	180	54	49	54	42	73.9
NMC 28485 Old Crow Loc. 143 (immature?).	110?	62	51	132	44	25	68	24	83.3?
							Average		93.3
<i>Alces alces</i> , Recent, Ontario**									
OR	108-	75-	65-	-	44-	43-	67-	46-	-
	189	105	100		67	58	80	49	
N	8	8	3	-	8	8	8	8	-

* 1 - Length of beam from burr to beginning of palmation.

2 - Maximum diameter of burr.

3 - Minimum diameter of burr.

4 - Circumference of beam directly distal to burr.

5 - Maximum diameter of beam (50 mm from burr).

6 - Minimum diameter of beam (50 mm from burr).

7 - Maximum diameter of beam (100 mm from burr).

8 - Minimum diameter of beam (100 mm from burr).

9 - Index of slenderness (%) $\left(\frac{\text{Measurement 1}}{\text{Measurement 4}} \times 100 \right)$. Slenderness is directly proportional to the % reading.

** I am grateful to C.S. Churcher for providing me with these measurements.

Table 79. Measurements of Pleistocene moose (*Alces alces*) maxilla and mandibles from the Yukon Territory compared to those of Recent moose from Canada.

Specimens	Estimated age of individual (years)	Sex	Measurements (mm)*														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Maxilla																	
<i>Alces alces</i> .Pleistocene, Y.T.																	
NMC 13548 Dawson Loc. 32	Adult	-	27.5	26.5	26.2	30.0	27.0	32.4	28.4	29.8	29.9	32.1	30.1	31.2	152.6	70.9	83.7
<i>Alces alces</i> .Recent, Canada																	
NMC 4840 Quebec	Adult	♂	25.2	25.2	24.0	28.3	25.7	30.6	33.1	27.5	29.6	30.0	31.1	30.4	152.0	71.2	81.6
NMC 4412 N.E.	Adult	♀	23.5	21.3	23.9	25.0	22.5	27.1	28.3	26.9	30.4	29.8	30.4	29.5	143.6	66.7	79.1
Mandibles																	
<i>Alces alces</i> .Pleistocene, Y.T.																	
NMC 11639 Dawson Loc. 32	5	-	21.1	14.5	24.7	17.7	28.2	21.8	28.8	22.8	30.4	23.5	39.2	23.2	166.6	73.1	94.0
LUM 1.3 Dawson Loc. 32	14+	-	19.3+	13.9	24.4	17.3	28.9	21.3	26.0	20.5	29.0	22.2	40.6	21.4	165.4	72.3	93.4
<i>Alces alces</i> .Recent, Canada																	
NMC 4840 Quebec	-	♂	19.8	14.9	23.8	16.5	25.9	19.0	30.5	19.1	30.4	21.8	38.6	22.3	166.0	71.9	93.8
NMC 4412 N.E.	-	♀	19.3	13.9	23.6	16.6	25.8	18.7	27.7	20.5	30.0	21.6	38.3	22.8	164.7	70.1	94.0

* 1 - Length P2.

2 - Width P2.

3 - Length P3.

4 - Width P3.

5 - Length P4.

6 - Width P4.

7 - Length M1.

8 - Width M1.

9 - Length M2.

10 - Width M2.

11 - Length M3.

12 - Width M3.

13 - Alveolar length P2-M3.

14 - Alveolar length P2-P4.

15 - Alveolar length M1-M3.

Table 80. Measurements of Pleistocene moose (*Alces alces*) radii and metatarsals from the Yukon Territory compared to those of Recent moose from Canada.

Specimens	Estimated age of individual	Sex	Measurements (mm)*						
			1	2	3	4	5	6	7
Radii									
<i>Alces alces</i> .Pleistocene, Y.T.									
NMC 11640 Dawson Loc. 32	-	-	420.0	80.7	50.7	45.0	29.9	75.2	59.5
NMC 11641 Dawson Loc. 32	-	-	-	-	-	40.0	30.0	72.1	54.8
<i>Alces alces</i> .Recent, Canada									
NMC 4850 Quebec	Adult	♂	425.0	82.1	51.1	47.9	-	79.3	60.4
NMC 4412 N.B.	Adult	♀	407.0	70.3	41.5	33.5	25.3	66.2	50.1
Metatarsals									
<i>Alces alces</i> .Pleistocene, Y.T.									
NMC 13546 Dawson Loc. 32	-	-	407.0	52.7	55.1	35.8	39.6	64.4	43.6
<i>Alces alces</i> .Recent, Canada									
NMC 4850 Quebec	Adult	♂	408.0	53.4	54.7	35.5	40.1	67.3	45.0
NMC 4412 N.B.	Adult	♀	385.2	46.4	47.7	27.1	31.2	58.6	38.8

* 1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Midshaft width.

5 - Midshaft depth.

6 - Distal width.

7 - Distal depth.

aid in separating moose from giant moose remains.

Occasionally, winter fecal pellets of moose have been collected from Pleistocene sediments in the Old Crow Basin.

Referred specimens

Referred left antlers - NMC 10474 from Dawson Locality 19 consists of an antler beam with the anterior half of the palmation bearing four tines. The tips of the tines and the posterior part of the antler base have been gnawed by rodents. Part of the pedicel is attached to the beam. The specimen is dark brown. NMC 10473 from the same locality consists of a shed antler. The anterior half of the palmation bearing five tines is attached to the beam. One tine projects ventrally from the base of the first cluster of four. As in NMC 10474, the proximal portion of the posterior half of the palmation is present. NMC 13547 from Dawson Locality 32 consists of a shed beam with the central part of the palmation. It is iron-stained. NMC 16255 from Old Crow Locality 18 is a shed antler with the central part of the palmation and the bases of anterior and posterior segments. NMC 27082 from Old Crow Locality 32E is relatively small, probably representing an immature male. I estimate that the proximal half of the palmation, including both anterior and posterior portions, is present.

Most of the dark brown outer surface of the antler has been eroded. NMC 11667 from Dawson Locality 13 consists of a shed beam with the proximal part of the palmation. Its light brown surface has darker patches. NMC 29003 from Dawson Locality 17 is an eroded antler beam with a small part of the palmation. The ventral surface extends farther into the palmation than does the dorsal surface. The specimen is stained brown. NMC 14006 from Old Crow Locality 1 is a deeply-stained beam with the proximal quarter of the palmation. It is attached to part of the left frontal bone. Probably the individual represented by the fossil died during autumn or early winter. NMC 17512 from Dawson Locality 32 is heavily weathered. A fragment of the anterior part of the palmation is attached to the beam. NMC 28527 from Old Crow Locality 143 consists of an unshed antler beam attached to a fragment of left frontal bone. The frontal shows the knob between the antlers that is typical of *Alces*. The surface of this heavily iron-stained fossil seems to have been pitted by acidic groundwater. Probably the animal represented by NMC 28527 died in autumn when the antlers had reached full maturity, but prior to winter when they are shed (Peterson 1966, p. 329). NMC 29002 from Dawson Locality 17 lacks the distal, upper portion of the antler beam. The lower segment extends into the

proximal part of the palmation. The specimen is stained brown.

Referred right antlers - NMC 25197 from Old Crow Locality 19 consists of a beam with the proximal half of the palmation. Although no tines are preserved, part of the inflection dividing the anterior from the posterior part of the palmation is present. The ventral surface is well preserved, showing details of the vascular pattern. NMC 29232 from Dawson Locality 13 consists of a heavily eroded beam with the proximal third of the palmation. It is attached to the frontal region of the cranium. Like NMC 28527, NMC 29232 represents an individual that probably died in autumn or early winter. The specimen is tan and may be of late Wisconsin age. NMC 17559 from Dawson Locality 32 is a shed beam lacking most of the palmation. NMC 16929 from near Johnson Village on the Porcupine River is a deeply iron-stained beam with the proximal part of the palmation. NMC 28485 from Old Crow Locality 143 is a small, well preserved beam. The beam gradually flattens and spreads laterally toward its distal extremity, so any measurement from the burr to the beginning of the palmation is arbitrary. This reddish brown antler fragment probably represents an immature male. NMC 17594 from Dawson Locality 28 is

a beam with a small part of the anterior portion of the palmation. It is dark brown.

It is worth noting that the slenderness index of Yukon Pleistocene *Alces alces* antlers averages approximately half that of *Alces latifrons* from the same region (Tables 77, 78). Ice age moose antlers from the Yukon differ little in size from those of modern Ontario moose.

NMC 13548 from Dawson Locality 32 is a right maxillary fragment with RP^2-RM^3 , part of the palatine process and most of the right malar and lacrimal bones. Among specimens of Recent moose to which it was compared, the fossil is closest to an adult male (NMC 4840).

Two mandibular fragments with teeth from Dawson Locality 32 also compare well with those of Recent moose. NMC 11639, part of a left mandible with LP_2-LM_3 , represents an individual of approximately 5 years of age according to Zaripov's aging system for Recent moose based on degree of wear of the mandibular tooth row (Heptner and Nasimowitsch 1967, p. 212). LUM 1.3 is a right mandibular fragment with RP_2-RM_3 . It seems to have been derived from an individual over 14 years of age.

Limb bones recovered at Dawson Locality 32 include a left radius with part of the ulna fused to the shaft (NMC 11640), and the distal half of a right radius (NMC 11641). These specimens are well matched by a Recent adult radius (NMC 4850). NMC 13546, a right metatarsal, also compares closely with the same bone from NMC 4850 - a mounted skeleton of a Recent moose. A left astragalus (LUM 1.169) compares well in maximum length, width and depth (72.9 mm x 49.8 mm x 39.4 mm) to that of a Recent adult moose from New Brunswick (NMC 4412) (73.5 mm x 48.5 mm x 40.4 mm).

Discussion

The deep staining and high degree of permineralization of some of the moose specimens (e.g. NMC 28527 and 28485) suggest a pre- late Wisconsin age. No fossils of *Alces alces* have been recovered from Unit 2 at Old Crow Locality 44, and no radiocarbon analyses have been carried out on moose remains from Eastern Beringia. However, *Alces alces* is a member of the Gold Run Creek fauna, which is of late Wisconsin age (approximately 22,000 to 32,000 years B.P.) (Harrington and Clulow 1973, p. 697), so the species probably occupied Eastern Beringia during the Wisconsin glaciation - a point that seems to be supported by the present distribution of moose subspecies in North America. Remains of moose have been

reported from postglacial deposits at Engigstciak near the northern Yukon coast (Mackay *et al.* 1961, p. 34).

The moose is not known from any of the major faunas in the rest of Canada (Harington 1976 MS.), but remains of Pleistocene to Recent age are recorded from: Saskatchewan (Pike Lake - ROM 5544; Pasqua - NMC 11317), Alberta (Rimbey - NMC 12231, an unusual digitate antler), British Columbia (McBride Creek - (Cowan 1941, p. 47); near Fort Nelson - NMC 13744). The deep iron-staining of the Fort Nelson specimen and the heavy permineralization of the partial antler from Rimbey suggest that they are of pre- postglacial age.

In the conterminous United States, *Alces alces* remains have been recorded from sites in Illinois, Kentucky, Michigan, Minnesota, Ohio, South Carolina, Washington and possibly a few other states. These specimens are either of uncertain age, or are definitely late Wisconsin to postglacial in age (B. Kurtén, personal communication 1976).

In Alaska, the earliest moose ("*Alces* sp. (moose)") record appears to be from loess of Illinoian age at Cripple Creek near Fairbanks (Péwé and Hopkins 1967, p. 268).

Fossils of *Alces alces* are fairly common in Wisconsin deposits of the Fairbanks region (Guthrie 1968b, Table 1). *Alces* sp., of possible late Wisconsin age or postglacial age, has been reported from the Tofty area (Repenning *et al.* 1964, p. 183). *Alces alces* has also been recorded from Eschscholtz Bay in western Alaska (Richardson 1854, p. 20). A complete frozen and untransported moose carcass was found in postglacial silt near Fairbanks according to J.L. Giddings (Péwé 1975a, p. 101).

Sher (1971, p. 197) mentioned the discovery of a metatarsal of "*Alces* sp." from the Utka Beds of Riss II (late Illinoian) age in the Kolyma Lowland of north-eastern Siberia. In size, it lay between modern *Alces alces* and *Alces latifrons*. In Siberia, moose remains are also known from late Pleistocene (Illinoian to Wisconsin?) sediments on Bolshoi Lyakhov Island. Regarding that record and other fossils of *Alces alces* in Siberia, Vangengeim (1961, p. 145) states: "It is known from numerous localities beginning from the end of the lower Pleistocene; remains of elk {moose} are encountered most frequently in the deposits of the upper Pleistocene. Of interest is the finding of a cast-off antler on Bolshoi Lyakhov Island, which perhaps

should be dated at the time of the climatic optimum {hypsihermal} of the Holocene, when the northern boundary of the forest occupied a maximal northern position." It is difficult to understand how the shed antler could date from the hypsihermal, however, for then sea water probably separated Bolshoi Lyakhov Island from the mainland. I think a time near the beginning of the late Wisconsin glaciation would be more likely for moose to be on that island. Moose are capable of moving far into tundra regions (Banfield 1974, Map 169).

According to Kurtén (1968, p. 169), *Alces alces* first appeared in Europe during the Riss (Illinoian) and was common there during the Eem (Sangamon) interglacial and the Würm (mid-Wisconsin) interstadial.

In summary, it seems that *Alces alces* evolved during the early Illinoian from a relatively small form of the giant moose (e.g. *Alces latifrons postremus*) that was adapting to life in the boreal forest, or in the more heavily wooded, marshy parts of parkland regions. Its dispersal centre may have been western Beringia. By the late Illinoian it had spread throughout the Holarctic from Siberia to Europe and to northwestern

North America. Presumably moose reached Eastern Beringia by moving through patches of boreal forest that may have existed in some of the more poorly drained areas on the Bering Isthmus. Evidently this species did not reach southern North America until mid-Wisconsin time (a Sangamon penetration is conceivable). During the last glaciation, probably moose were isolated in at least two main areas of boreal forest south of the ice, as well as in Eastern Beringia. Probably *Alces alces americana* subspeciated in the northeastern United States, *Alces alces shirasi* in the northwestern United States, and *Alces alces gigas* in Eastern Beringia (Peterson 1955, p. 14). Youngman (1975, p. 161) considers that *Alces alces andersoni* is an intergrade between *Alces alces gigas* and adjacent southern subspecies. At present, moose occur throughout the Yukon Territory; they are common in both the Dawson and Old Crow areas.

Moose now occupy boreal forest belts across northern Eurasia from Scandinavia to the Pacific coast, and across North America from Alaska to Maine and Newfoundland. They are the largest living deer. Males weigh 725-1,400 pounds (329-635 kg) and females 500-900 pounds (227-408 kg). The moose is characterized by its long face with overhanging muzzle, unusually long legs, and in males, large palmate antlers. Moose prefer boreal

forest - especially areas of second growth or intermediate stages of forest succession interspersed with lakes and streams - and its fossils are probably good paleoenvironmental indicators of such conditions. This suggests to me that some areas of boreal forest have existed in Eastern Beringia throughout the late Pleistocene, no matter how bleak some of the pollen records from central and western Alaska may appear. According to available data, it appears that moose and their probable ancestors the giant moose lived together in Eastern Beringia - although probably the giant moose arrived earlier. I suggest that *Alces latifrons* occupied the open steppe-like or parkland regions, while *Alces alces* was mainly concentrated in more densely wooded, marshy regions within the refugium.

Moose are relatively solitary, however, they sometimes congregate in marshy areas that produce good forage. Their long legs allow them to move well in deep snow that often gathers in the boreal forest. They are excellent swimmers and spend more time in the water than most deer. Moose seek out aquatic vegetation during the summer, in addition to their basic diet of broad-leaved trees and shrubs (e.g. willow). In winter, balsam fir is an important food. These large animals require about 5 pounds (2.3 kg) of browse per hundred pounds of moose per day (i.e. approximately 50 pounds (22.7 kg) per day for a medium-sized bull). Wolves are the

main predators of the moose. They are adept at weeding out old, weak and younger animals. Brown bears are sometimes able to prey on cows and calves in spring, and black bears can run fast enough to catch moose calves (Peterson 1966, pp. 326-329; Banfield 1974, p. 396).

Rangifer tarandus (caribou)

Caribou remains (Figures 72b, 73A-B, 74A-B, Tables 81-84) are among the most common from Yukon Pleistocene deposits. Of hundreds of specimens collected, only the more complete antlers, cranial fragments and metapodials are described. Most antlers are of the cylindrical type that presently characterize the barren-ground subspecies. The fossil evidence from Old Crow suggests that caribou occupied that area throughout the late Pleistocene, perhaps from Illinoian time to the present.

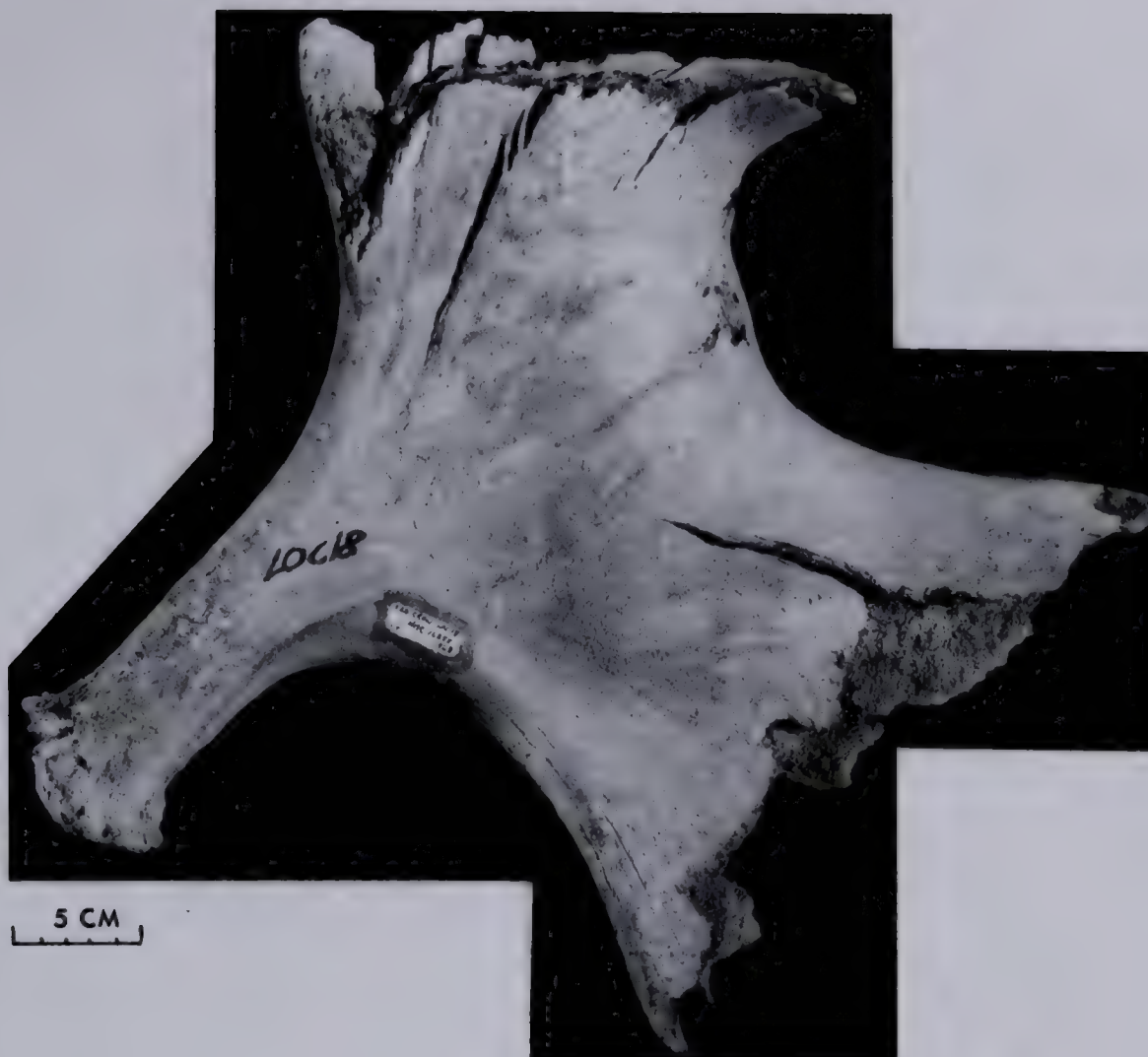
Antlers are common in the collection. Most consist of the proximal half of the beam with broken tines and were shed.

Referred specimens

Referred left antlers - NMC 13538 from Dawson Locality 32 is a buff-colored, shed antler that is complete except for the tips of the tines. A keel is formed in place of the first posterior tine. Proximal portions of the second and third posterior tines are present. A 650 mm segment of beam is



Figure 72. A. Dorsal view of a left antler fragment
(NMC 16255, Old Crow Locality 18) of a
Pleistocene moose (*Alces alces*).
B. Medial view of a left antler (NMC 13538,
Dawson Locality 32) of a Pleistocene
caribou (*Rangifer tarandus*).



A



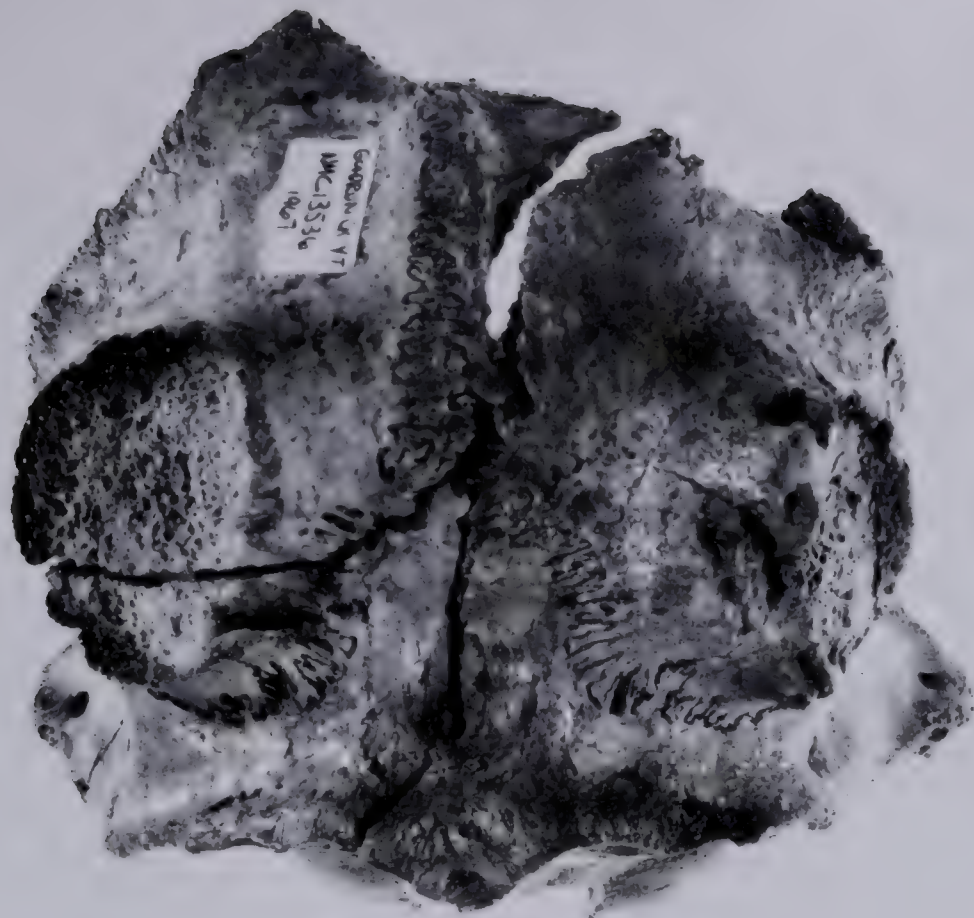
B



Figure 73. Posterior cranial fragment (NMC 13536,
Dawson Locality 32) of a Pleistocene
caribou (*Rangifer tarandus*).

A. Dorsal view. Note circular antler
pedicel areas on either side of the
frontal suture.

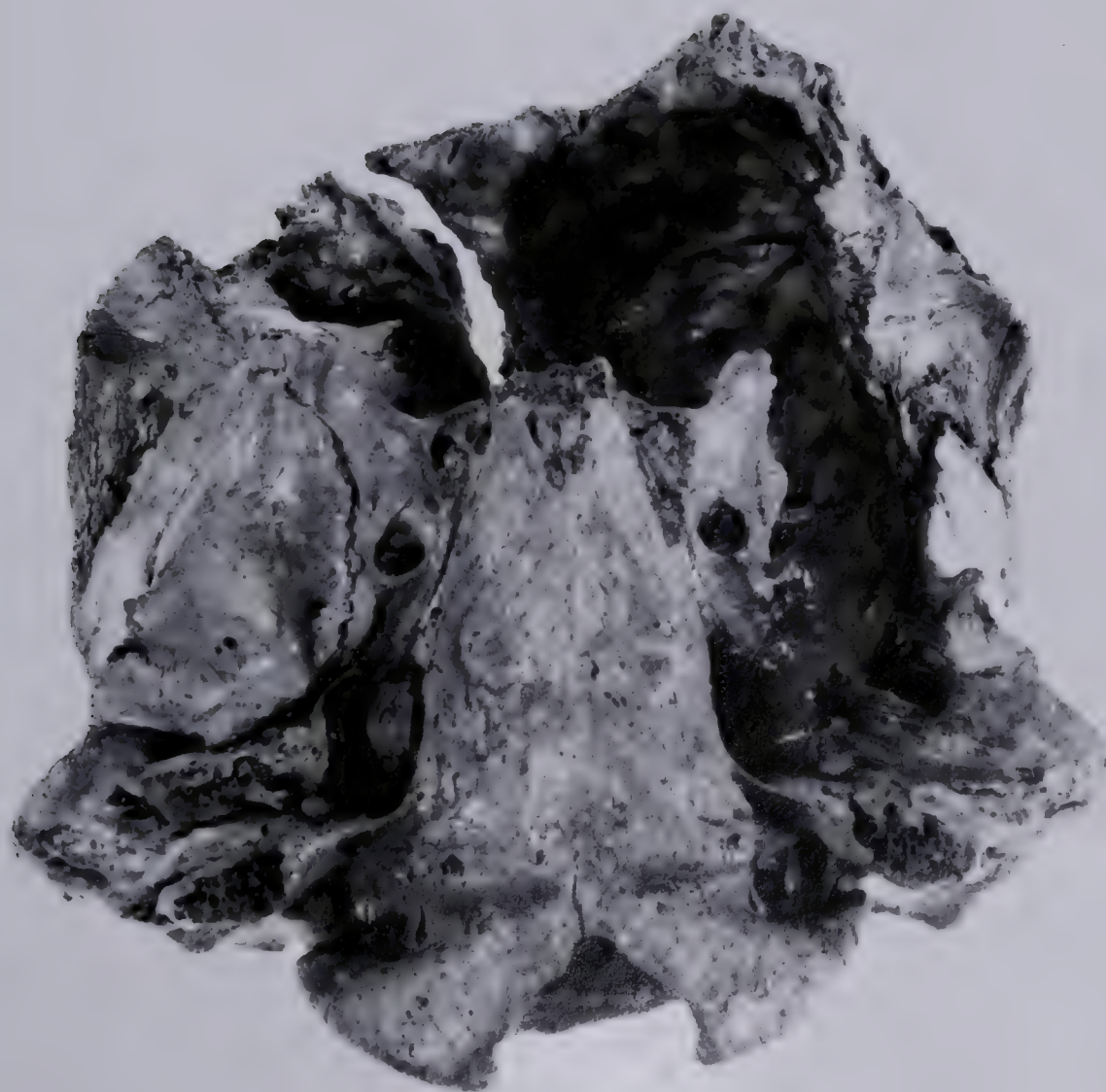
B. Ventral view.



5 CM

A

5 CM



B

Figure 74. Right mandible with RP_2 - RM_3 (NMC 24211, Old Crow Locality 12) of a Pleistocene caribou (*Rangifer tarandus*).

- A. Lateral view.
- B. Occlusal view.

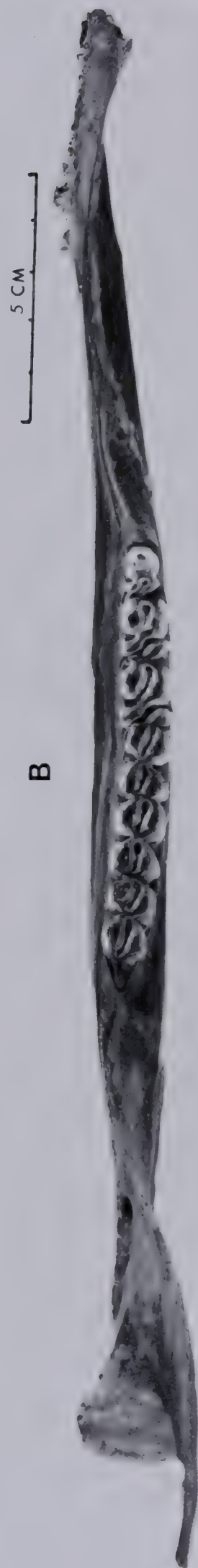
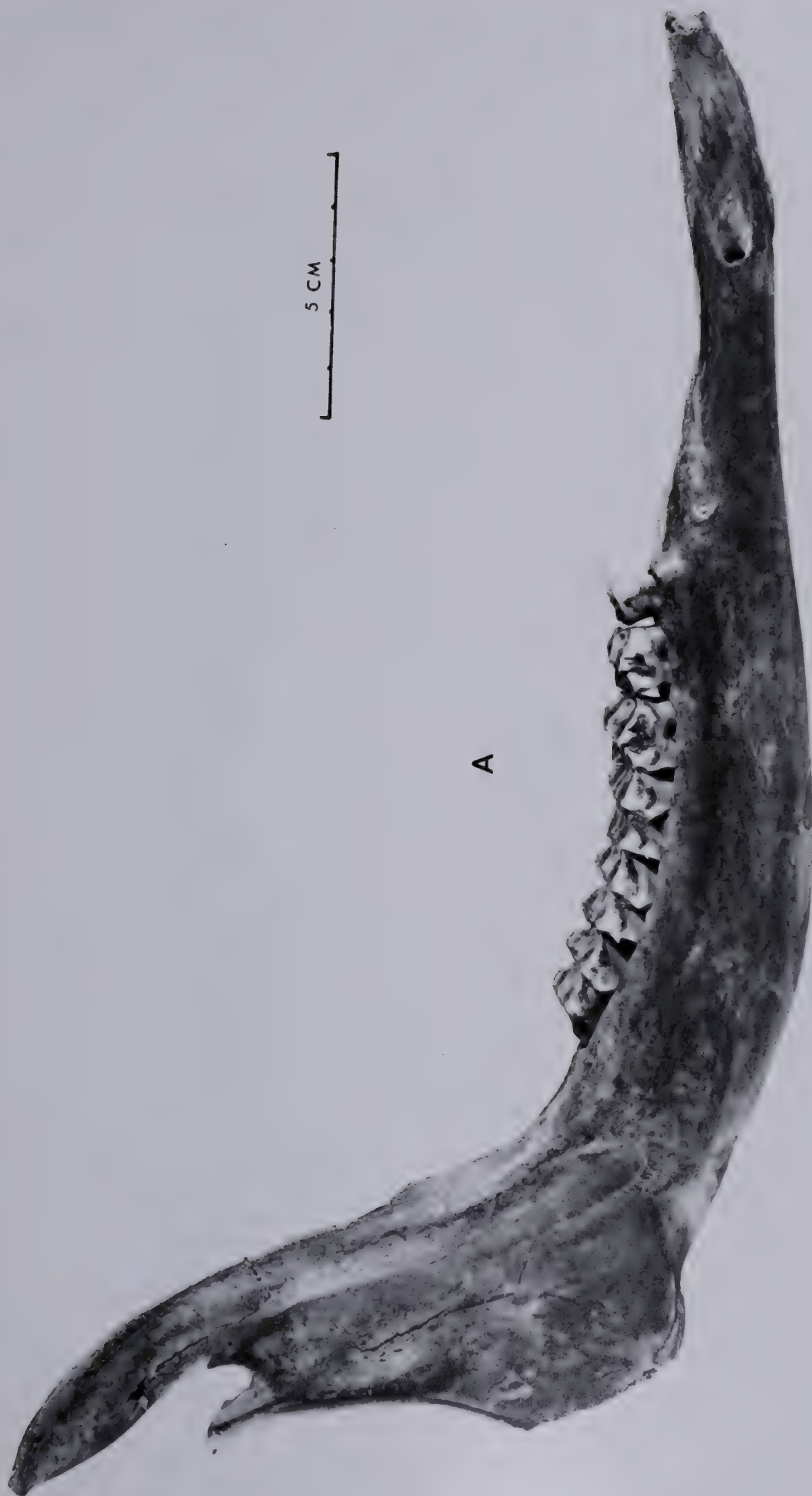


Table 81. Measurements of Pleistocene caribou (*Rangifer tarandus*) antlers from the Yukon Territory.

Specimens		Measurements (mm) *						
		1	2	3	4	5	6	7
<i>Rangifer tarandus</i> , Pleistocene, Y.T.								
NMC 13538 Dawson Loc. 32		47.7	45.4	71.3	40.5	46.3	39.8	270e
NMC 13539 Dawson Loc. 32		39.0	32.6	45.0	33.8	40.3	32.4	260
NMC 13543 Dawson Loc. 32		45.9	40.0	47.8	33.3	37.8	34.4	-
NMC 13544 Dawson Loc. 32		36.0	27.8	37.0	24.2	29.5	27.7	225
NMC 11643 Dawson Loc. 32		45.3	39.1	40.7	32.7	37.7	35.2	-
NMC 13540 Dawson Loc. 32		49.0	41.7	40.6	33.5	-	-	-
NMC 20838 Old Crow Loc. 11A		50.0	38.5	42.5	32.0	35.8	31.9	340
NMC 17320 Dawson Loc. 7		50.6	44.7	44.2	38.4	36.4	36.4	-
NMC 14009 Old Crow Loc. 3		40.6	34.6	36.2	28.8	33.2	26.7	340
NMC 17195 Old Crow Loc. 11		60.9	50.4	45.2	36.8	45.0	34.8	360
NMC 25926 Dawson Loc. 16		47.8	39.3	45.4	33.1	43.7	32.9	360
NMC 25925 Dawson Loc. 16		47.4	41.4	39.8	32.8	33.3	33.8	-
NMC 11724 Dawson Loc. 28		43.0	41.4	50.2	39.2	41.3	37.5	380
NMC 11334 Dawson Loc. 25		49.2	43.1	43.3	37.0	47.9	36.0	275
NMC 28583 Old Crow Loc. 71		39.3	35.3	44.8	30.1	32.9	29.0	-
NMC 17595 Dawson Loc. 28		40.0	33.3	33.3	29.9	30.5	27.5	270
NMC 20839 Old Crow Loc. 11A		43.4	36.0	40.7	32.0	35.0	29.6	-
NMC 20454 Old Crow Loc. 20		55.2	39.5	-	-	39.8	35.9	-
NMC 17907 Dawson Loc. 32		46.8	37.6	48.4	35.0	46.3	30.6	390
NMC 18198 Old Crow Loc. 44		41.3	35.4	39.0	31.1	34.3	31.1	-
NMC 11335 Dawson Loc. 25		48.3	42.1	44.7	36.4	44.8	36.2	270
NMC 28955 Old Crow Loc. 22		47.8	43.6	44.9	35.8	45.2	33.5	440e
NMC 25260 Peel Plateau Loc. 1		35.6	30.6	38.0	29.5	34.7	29.3	-
NMC 7752 Dawson Loc. 9		51.6	41.3	53.2	39.1	50.0	37.2	265
NMC 14848 Old Crow Loc. 27		33.3	28.0	-	-	31.7	25.9	350
NMC 20128 Old Crow Loc. 74		51.0	40.9	45.5	32.6	42.6	31.0	-
NMC 23207 Old Crow Loc. 27		43.1	37.3	38.2	30.8	33.8	29.5	-
NMC 14933 Porcupine Loc. 35		34.0	28.9	38.5	27.0	35.8	26.2	290
NMC 25213 Dawson Loc. 29		35.5	26.6	41.6	23.5	28.3	24.0	275
NMC 17357 Dawson Loc. 2		45.9	45.7	42.0	33.7	39.5	-	-
NMC 29019 Dawson Loc. 16		47.0	44.0	52.5	42.5	42.0	36.3	-
NMC 11347 Dawson Loc. 2		39.6	39.1	37.9	32.8	35.1	31.3	-
NMC 29138 Sixtymile Loc. 3		38.9	35.3	39.4	27.8	29.7	27.3	-
NMC 24197 Old Crow Loc. 82		33.4	31.1	38.1	25.9	-	-	-
NMC 23208 Old Crow Loc. 133		41.9	38.4	41.2	33.3	39.0	29.7	-
NMC 26880 Old Crow Loc. 22		48.7	37.6	-	-	37.2	37.3	-
NMC 14347 Old Crow Loc. 14N		38.9	40.0	-	-	35.5	32.0	-
NMC 16465 Old Crow Loc. 53		47.1	45.2	47.3	40.2	45.7	34.8	-
NMC 27403 Old Crow Loc. 81		43.2	42.2	43.7	46.5	40.0a	35.4	-
NMC 27450 Old Crow Loc. 65S		34.2	27.6	32.2	21.3	-	-	-
NMC 25965 Old Crow Loc. 25		31.7	25.4	31.2	20.9	23.6	20.3	-
NMC 26796 Old Crow Loc. 20		40.4	34.3	43.6	33.9	-	-	-
NMC 28343 Old Crow Loc. 136		36.5	34.0	35.2	31.2	-	-	-
NMC 27081 Old Crow Loc. 32E		44.4	41.9	46.8	36.1	41.9	36.3	-
NMC 27953 Old Crow Loc. 114		37.3	35.2	34.6	36.1	34.9	29.9	-
NMC 29137 Sixtymile Loc. 3		21.6	19.7	20.5	15.8	-	-	-

- * 1 - Anteroposterior diameter of antler base (or pedicel below burr, if antler is attached to cranium).
 2 - Mediollateral diameter of antler base (or pedicel below burr, if antler is attached to cranium).
 3 - Minimum anteroposterior diameter of beam between first (brow) and second (bez) anterior tines.
 4 - Minimum mediollateral diameter of beam between first and second anterior tines.
 5 - Anteroposterior diameter of beam 100 mm distal to the centre of the second anterior tine.
 6 - Mediollateral diameter of beam 100 mm distal to the centre of the second anterior tine.
 7 - Straight line distance from posterior of burr to centre of base of first posterior tine (where present).

Table 82. Measurements of Pleistocene caribou (*Rangifer tarandus*) crania from the Yukon Territory compared to those of Recent caribou from North America.

Specimens	Sex	Measurements (mm)*							
		1	2	3	4	5	6	7	8
<i>Rangifer tarandus.</i>									
Pleistocene, Y.T.									
NMC 13536 Dawson Loc. 32	♂	90.6	100.8	61.0	84.2	70.8	42.6	102.0	114.0e
LUM 1.16 Dawson Loc. 32	-	88.5	87.2	53.9	74.5	65.3	41.5	102.0	101.1
NMC 14905 Old Crow Loc. 31	♂	72.0	97.0	55.4	86.0	76.7	46.0	104.6	-
NMC 25924 Dawson Loc. 16	-	74.0	93.0	55.9	81.3	68.1	42.3	94.9	-
NMC 25179 Dawson Loc. 16	♂	79.0	-	61.5	-	69.4a	-	105.3	119.9
NMC 16368 Old Crow Loc. 66	-	67.2a	84.6a	51.3a	73.6a	70.7	44.5	-	-
NMC 13621 Old Crow Loc. 2	-	70.8a	92.3a	59.0	85.2	69.2	42.0a	-	-
NMC 25183 Dawson Loc. 16	♂	-	-	-	-	-	-	95.0e	106.5
NMC 17400 Sixtymile Loc. 1	♂	-	-	-	-	-	-	109.3	120.3
NMC 14016 Old Crow Loc. 2	-	-	-	-	-	68.3	44.5	-	-
NMC 27807 Old Crow Loc. 83	-	-	-	-	-	68.5	47.6	-	-
NMC 25968 Dawson Loc. 29	-	-	-	-	-	-	-	99.1	-
<i>Rangifer tarandus granti.</i>									
Recent, N. America									
NMC 22803 Alaska	♂	91.2	101.1	60.3	80.6	69.6	43.4	100.0	102.4
NMC 2270 Y.T.	♂	89.5	107.0	62.1	88.6	82.8	52.4	102.0	96.9
NMC 2263 Y.T.	♀	78.0	96.2	53.1	80.2	73.9	43.2	94.6	94.6
<i>Rangifer tarandus groenlandicus.</i>									
Recent, N. America									
NMC 24326 N.W.T.	♂	93.5	105.6	63.4	88.7	67.8	52.7	107.6	113.1
NMC 22111 Man.	♀	79.9	82.1	71.6	70.8	67.8	42.1	87.6	87.9
NMC 22104 N.W.T.	♀	72.0	80.3	49.1	72.3	62.6	39.1	86.6	91.1
<i>Rangifer tarandus pearyi.</i>									
Recent, N. America									
NMC 22827 N.W.T.	♂	74.9	87.0	55.8	89.9	63.7	40.4	89.3	95.4

* 1 - Cranial height, dorsal lip of foramen magnum to highest point on frontal suture between antler pedicels.

2 - Cranial height, ventral margin of occipital condyle to highest point on frontal suture between antler pedicels.

3 - Occipital height, dorsal lip of foramen magnum to top of nuchal crest.

4 - Occipital height, ventral margin of occipital condyle to top of nuchal crest.

5 - Maximum width across occipital condyles.

6 - Maximum width across posterolateral margins of basioccipital.

7 - Minimum width of cranium below and just posterior to antler pedicels.

8 - Minimum width across frontals immediately anterior to antler pedicels.

Table 23. Measurements of Pleistocene caribou (*Rangifer tarandus*) mandibles compared to those of Recent caribou from North America.

Specimens	Sex	Estimated Age (years)	Measurements (mm)*															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Fragilaria tarandus</i> , Pleistocene, Y.T.																		
NMC 14339 Old Crow Loc. 14N	-	6	28.8	14.7	54.6	10.1	7.5	15.0	10.6	17.3	11.5	10.9	9.6	19.3	11.0	21.9	10.1	97.5
NMC 29650 Dawson Loc. 30	-	14	28.8	14.3	-	7.6 [†]	6.2 [†]	14.1	-	14.6	11.0	16.9	10.1	18.7	11.2	26.2e	10.7	98.6e
NMC 28737 Old Crow Loc. 11	-	5	31.8	15.8	39.9	12.3	8.9	16.2	11.3	18.3	13.1	18.8	11.0	-	-	-	-	-
NMC 14991 Old Crow Loc. 69	-	4	-	17.0	-	-	-	-	-	-	-	20.8	11.8	21.9	12.4	23.4	11.2	-
NMC 22869 Old Crow Loc. 11A	-	15	-	15.2e	-	-	-	14.1	10.7	16.7	11.4	16.0	9.7	12.9	10.9	-	-	-
NMC 17083 Old Crow Loc. 8	-	4	29.1	15.4	47.2	-	-	-	-	-	-	-	-	-	-	-	-	108.2e
NMC 26591 Old Crow Loc. 11A	-	2	-	13.8	50.4**	-	-	11.1**	6.7**	19.5**	8.6**	17.6	9.6	18.8	10.5	22.0	-	100.6e**
NMC 13607 Old Crow Loc. 11A	-	1.5a	24.5	12.6	42.5**	8.4**	4.8**	12.3**	6.5**	19.4**	7.9**	18.2	9.2	-	-	-	-	-
NMC 26976 Old Crow Loc. 22	-	.25	23.6	12.6	-	8.9**	4.7**	13.9**	6.8**	23.0**	9.1**	-	-	-	-	-	-	-
NMC 29739 Old Crow Loc. 4	-	.17	20.3	11.9	-	9.0**	4.4**	13.5**	7.1**	22.2**	9.0**	-	-	-	-	-	-	-
<i>Fragilaria tarandus</i> , Recent, Alaska																		
NMC 22207	♀	3.5	29.3	13.5	52.0	10.0	7.1	14.1	9.2	16.0	10.4	17.2	9.0	18.3	9.8	23.5	10.2	98.0
<i>Fragilaria tarandus groenlandicus</i> , Recent, N.W.T. (Miller 1974, Tables 7, 8)																		
<u>Males</u>																		
M	♂♂	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	97.0
N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	236
SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.8
<u>Females</u>																		
M	♀♀	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	95.7
N	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	334
SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.4

* 1 - Mandibular depth at centre of M₁.

2 - Mandibular width at centre of M₁.

3 - Length from anterior of P₂ alveolus to posterior of mental foramen.

4 - P₂ length.

5 - P₂ width.

6 - P₃ length.

7 - P₃ width.

8 - P₄ length.

16 - P₂-M₃ alveolar length.

** Measurements taken on deciduous teeth or from alveoli of deciduous teeth.

Table 84. Measurements of Pleistocene caribou (*Rangifer tarandus*) metapodials from the Yukon Territory compared to those of Recent caribou from Alaska and the Northwest Territories.

Recent collected from Alaska and the Northwest Territories.

Specimens	Sex	Measurements (mm)*						
		1	2	3	4	5	6	7

Metacarpals

Rangifer tarandus.
Pleistocene, Y.T.

NMC 26690 Old Crow Loc. 27W	-	218.4	38.4	28.6	25.6	26.4	46.0	24.6
NMC 14698 Old Crow Loc. 28	-	214.7	37.2	26.9	22.9	21.5	44.2	24.3
NMC 15268 Old Crow Loc. 22	-	208.7	37.0	28.0e	20.1	21.8	45.3	23.2 ⁺
NMC 29126 Sixtymile Loc. 3	-	200.3	34.9	26.3	19.4	21.4	43.6	22.2
NMC 29125 Sixtymile Loc. 3	-	197.5	35.0	25.2	21.9	21.3	43.1	23.2
NMC 26774 Old Crow Loc. 20	-	197.3	33.8	23.9	20.3	20.0	42.2	22.1
NMC 15356 Old Crow Loc. 14N	-	196.7	38.4	27.9	23.9	23.7	45.3	23.8
NMC 25242 Dawson Loc. 2	-	194.1	36.2	26.8	18.6	21.3	43.6	23.3

Rangifer tarandus.
Recent, Alaska

NMC 32207	♀	215.8	35.9	26.7	21.3	19.9	45.9	25.2
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Metatarsals

Rangifer tarandus.
Pleistocene, Y.T.

NMC 14950 Eagle Loc. 37	-	292.7	31.2	36.2	27.9	30.2	43.9	25.0
NMC 13537 Dawson Loc. 32	-	279.0	32.2	35.0	24.4	32.9	43.5	21.6 ⁺
NMC 29251 Old Crow Loc. unknown	-	257.1	-	-	17.0	21.6	34.5 ⁺	20.0 ⁺
NMC 17248 Dawson Loc. 28	-	255.3	27.1	32.3	19.8	29.0	39.2	21.2

Rangifer tarandus.
Recent, N. America

NMC 32213 Alaska	♀	291.6	35.7	38.9	25.0	37.1	47.5	26.5
NMC 22972 N.W.T.	♂ ⁺	267.4	31.1	35.7	26.3	34.7	42.4	24.8
NMC 22980 N.W.T.	♂ ⁺	261.4	29.3	31.9	20.0	28.7	40.7	23.0
NMC 22978 N.W.T.	♂ ⁺	255.3	29.5	33.5	23.2	30.3	41.2	23.1

*1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Midshaft width.

5 - Midshaft depth.

6 - Distal width.

7 - Distal depth.

preserved. The specimen is on display in the National Museum of Natural Sciences, Ottawa. NMC 27953 from Old Crow Locality 114 is a shed antler with stubs of the brow (first anterior) and bez (second anterior) tines. A 190 mm segment of beam is preserved. The specimen is stained orange-brown. NMC 27081 from Old Crow Locality 32E is a shed antler with stubs of the brow and bez tines. A 240 mm segment of beam is preserved. It is stained black. NMC 28343 from Old Crow Locality 136 is a shed antler with the stub of the brow tine and approximately a quarter of the bez tine. A 190 mm segment of beam is preserved. The surface of the fossil is pitted. It is stained dark brown. NMC 26796 from Old Crow Locality 20 is a shed antler with proximal halves of the brow and bez tines. The beam, of which 190 mm is preserved, is compressed laterally and spreads anteroposteriorly between the tines, approaching the woodland caribou form. The surface of the specimen is deeply pitted and is stained brownish black. NMC 17357 from Dawson Locality 2 is a shed antler with a stub of the brow tine and about half of the bez tine (which seems to have been gnawed at the distal extremity). The brow and bez tines are relatively far apart (160 mm). Pyrolusite "stars" are seen on the medial surface. A 290 mm segment of beam is preserved. NMC 25213 from Dawson Locality 29 is a shed antler with stubs of the brow, bez and first posterior tines. A 330 mm segment of beam is preserved. Material in cracks suggests that the fossil was deposited in a peat layer.

NMC 13540 from Dawson Locality 32 is a shed antler with proximal halves of brow and bez tines. A 290 mm segment of beam is preserved. It is rust colored. NMC 25260 from Peel Plateau Locality 1 is a shed antler with a stub of the brow tine, and the proximal third of the bez tine. An incipient tine is evident on the lateral surface at the level where a first posterior tine is usually found. A 580 mm segment of the beam is preserved. It was not found in place, but S.C. Zoltai, who collected it, remarked that it was probably from a peat layer of Pleistocene age. NMC 13539 from Dawson Locality 32 is a shed antler with proximal thirds of the brow and bez tines and the base of the first posterior tine. A 480 mm segment of the beam is preserved. It varies from orange-brown to black. NMC 20839 from Old Crow Locality 11A is attached to a small part of the cranium. The distal half of the brow tine and most of the bez tine is lacking. A 300 mm segment of beam is present. The fossil is brownish black and has been deeply pitted by acids in the groundwater. The pits are mainly concentrated on the dorsal surface. NMC 28583 from Old Crow Locality 71 is a shed antler with complete (300 mm long) brow tine. The tip of the bez tine is missing and no first posterior tine or keel is developed. A 740 mm segment of beam is preserved. The specimen is stained

dark brown. NMC 11724 from Dawson Locality 28 is a shed antler with the stub of the brow tine, a large bez tine lacking the tip, and the stub of a small, laterally compressed first posterior tine. A 580 mm segment of beam is preserved. It is light buff to tan.

NMC 25925 from Dawson Locality 16 is a shed antler with a stub of the brow tine, and about half of the bez tine. A 430 mm segment of beam is preserved. A first posterior tine is not present. The fossil is dark

tan. NMC 14009 from Old Crow Locality 3 is a heavily weathered, iron-stained antler beam with attached cranial fragment. The stub of the brow tine and the proximal third of the bez tine are present. The first posterior tine is very small. NMC 20838 from Old Crow Locality 11A consists of most of a beam fused to a small cranial fragment. The distal half of the brow tine and the end of the bez tine are missing. A keel is developed in place of the first posterior tine. A 600 mm segment of beam is preserved. The fossil is stained rusty brown.

Referred right antlers - NMC 11643 from Dawson Locality 32 consists of most of a tan colored antler beam fused to a cranial fragment. The stub of the brow tine and half of the bez tine are present. A 600 mm segment of beam is preserved. NMC 17320 from

Dawson Locality 7 consists of most of a tan colored shed antler, lacking the ends of brow and bez tines. The bez tine has deep gnaw marks. A broad ridge, but not a keel, is developed in place of a first posterior tine. A 720 mm segment of beam is preserved. Fine rootlet impressions cross the surface of the fossil. NMC 17195 from Old Crow Locality 11 consists of an antler beam attached to a cranial fragment. The tips of brow and bez tines are missing. A small, incipient tine is located 20 mm distal to the bez tine. The tip of the first posterior tine is lacking. A 420 mm segment of beam is preserved. The specimen is stained deep brown. NMC 25926 from Dawson Locality 16 is a shed antler with only the stubs of brow, bez and first posterior tines. It is stained light, reddish brown, and has been radio-carbon dated at $23,900 \pm 470$ years B.P. (I-8580), which tends to support the idea that caribou were present near Dawson near the peak of the last glaciation. NMC 11334 from Dawson Locality 25 is a shed antler with most of a well developed brow tine. Approximately two-thirds of the bez tine, and the stub of the first posterior tine are present. A 440 mm segment of beam is preserved. The fossil is stained deep brown. NMC 17595 from Dawson Locality 28 is a shed antler with stubs of brow and bez tines. A keel is developed in place of the first posterior

tine. A 600 mm segment of beam is preserved. It is stained dark rust. NMC 20454 from Old Crow Locality 20 is a shed antler with short portions of the brow and bez tines - which, in this specimen, originate at the same point near the burr. A 420 mm segment of beam is preserved. The surface of the specimen is stained light rusty brown. NMC 17907 from Dawson Locality 32 is a shed antler with a stub of the brow tine and the proximal half of the bez tine. The base of the laterally compressed first posterior tine is present. Gnaw marks are seen on the surface of the beam opposite the first posterior tine, and on the bez tine. NMC 18198 from Old Crow Locality 44 is a shed antler with a stub of the brow tine and the proximal half of the bez tine. The beam is relatively straight, and there is no evidence of a first posterior tine. A 450 mm segment of beam is preserved. Although this fossil was not in place in Unit 2, other caribou remains were collected from that unit, which may be of Sangamon interglacial age. NMC 18198 was evidently derived from a peat deposit, for peat adhered tightly to most of its surface. Samples of this peat were taken for identification. NMC 11335 from Dawson Locality 25 is a shed antler with a stub of brow tine, half of a well developed bez tine, and the stub of a small first posterior tine. A 470 mm segment of beam is preserved.

The surface of the specimen is rust colored. NMC 28955 from Old Crow Locality 22 is a shed antler with a third of the brow tine, two-thirds of a well developed bez tine and part of a small first posterior tine. A 680 mm segment of beam is preserved. NMC 7752 from Dawson Locality 9 is a short, robust, laterally compressed, shed antler. It appears to be more like woodland caribou than tundra caribou antlers (Banfield 1961, p. 34). The brow tine is broken near the base and approximately a quarter of the large, flattened bez tine is preserved. The first posterior tine is poorly developed. A 360 mm segment of beam is present. Gnaw marks are evident on the beam near the first posterior tine. NMC 13543 from Dawson Locality 32 is a shed antler with the stubs of brow and bez tines. A 350 mm segment of beam is preserved. The specimen is rusty brown in color. NMC 14848 from Old Crow Locality 27 is a shed antler with the stub of a laterally compressed brow tine. No bez tine is developed. the first posterior tine is heavily eroded. A 590 mm segment of beam is preserved. It is stained dark brown. NMC 20128 from Old Crow Locality 74 is a brownish black, shed antler with a trace of the brow tine and approximately half of the bez tine. A 420 mm segment of beam is preserved. NMC 23027 from Old Crow Locality 27 is a shed antler with a stub of the brow tine, and a quarter of the bez tine. It

should be examined by archeologists, for the brow tine may have been cut off. Part of a slanting, polished facet is preserved on the medial surface of the stub. A 400 mm segment of beam is preserved. NMC 13544 from Dawson Locality 32 is a heavily iron-stained, shed antler with approximately half of the brow tine and the stub of the bez tine. Damage to the beam may have resulted in its abnormal lateral convexity between the bez and first posterior tines. A 300 mm segment of beam is preserved. NMC 14933 from Porcupine Locality 35 is a dark brown shed antler. Both brow and bez tines are broken near their points of origin. A stub of the first posterior tine is present. A 380 mm segment of beam is preserved. NMC 29019 from Dawson Locality 16 is a shed antler with approximately a third of the brow tine and half of the bez tine. A 230 mm segment of beam is preserved. It is stained orange-brown. NMC 11347 from Dawson Locality 2 is a shed antler with halves of the brow and bez tines. A 240 mm segment of beam is preserved. It is grayish buff. NMC 29138 from Sixtymile Locality 3 has a stub of the brow tine and approximately half of the bez tine. The antler beam, of which 250 mm is preserved, is attached to a small cranial fragment. NMC 24197 from Old Crow Locality 82 is an antler with two-thirds of the brow and bez tines. It is attached to a fragment of the

braincase. A 140 mm segment of beam is preserved.

NMC 23208 from Old Crow Locality 133 is a shed antler with only a nubbin in the position of the brow tine, and a stub of a large bez tine. The posterior edge of the antler base may be faceted. A 250 mm segment of beam is preserved. The fossil is dark brown to black. NMC 26880 from Old Crow Locality 22 is a heavily iron-stained antler with brow and bez tines having the same point of origination above the burr. Possibly half of the brow tine is present. The bez tine is broken near its source on the beam. The antler is attached to a small cranial fragment. The distal 85 mm of the beam was heavily gnawed by a medium-sized to large carnivore. NMC 14347 from Old Crow Locality 14N is an antler with the stub of a brow tine. No bez tine is seen. The antler is attached to a fragment of the braincase. A 200 mm segment of beam is preserved. It is stained orange-brown. NMC 16465 from Old Crow Locality 53 is a shed antler with stubs of brow and bez tines. It is stained a light rust color. NMC 27043 from Old Crow Locality 81 is a shed antler with part of the brow tine and a stub of the bez tine. The distal part of the bez tine was gnawed. A 190 mm segment of beam is preserved. It is stained dark brown. NMC 27540 from Old Crow Locality 65S is a small, heavily eroded, shed antler with stubs of brow and bez tines. A 150 mm segment of beam is preserved.

It is dark brown. NMC 25965 from Old Crow Locality 25 is a shed antler. The brow tine has been broken off at the base, and approximately a quarter of the bez tine is present. A 260 mm segment of beam is preserved. It is stained reddish brown. NMC 29137 from Sixtymile Locality 3 is a shed antler of a female. It lacks a brow tine, but most of the bez tine is present. A 150 mm segment of beam is preserved. It is light buff. Because female antlers are dropped during the calving period, this specimen indicates that some caribou calving occurred in the Sixtymile area during the late Wisconsin.

The fact that 33% of 24 male caribou antlers sampled from the Old Crow - Porcupine region were unshed and that 10% of 20 male antlers sampled from the Dawson - Sixtymile region were unshed suggests that many male caribou were present in both regions during the winter (when they drop their antlers) and that more bucks died in the late summer or autumn (when their antlers are well developed) in the Old Crow - Porcupine region than in the Dawson - Sixtymile region. Possibly a number of these deaths occurred during the rutting period.

Several cranial fragments are in the collections from the Yukon. NMC 13536 from Dawson Locality 32 lacks

antlers and bone anterior to the orbits. It is cracked near the frontal suture. Apparently the antlers were shed not long before the death of the individual represented. Maximum diameter of the antler scars is approximately 50 mm. NMC 13536 is comparable in size to crania of Recent adult male barren-ground caribou (NMC 22808, 24326). It is tan in color. LUM 1.16 from Dawson Locality 32 also lacks antlers and bone anterior to the orbits.

NMC 14905 from Old Crow Locality 31 is a posterior cranial fragment. It represents a male according to the large diameter (55 mm) of the antler scars. The relatively high degree of fusion of the frontal suture suggests that the fossil represents an animal in advanced adulthood. Occipital and basioccipital surfaces are minutely pitted, probably due to acids in the groundwater. NMC 14905 is dark brown. NMC 25924 from Dawson Locality 16 is a posterior cranial fragment lacking the entire bottom of the braincase and the left occipital condyle. The frontal extends approximately 40 mm forward from the supraorbital foramina. Maximum diameter of the antler scars is about 42 mm. The bone is tan.

NMC 25179 from Dawson Locality 16 is a posterior

cranial fragment with eroded occipital margins. Maximum diameter of the antler scars is 34 mm. The fossil is stained orange-buff. NMC 16368 from Old Crow Locality 66 is a cranial fragment lacking bone anterior to the antler pedicels. The dorsal surface of the fragment is heavily eroded, and parts of the left side of the occiput are lacking, including much of the left occipital condyle. It is stained reddish brown.

NMC 13621 from Old Crow Locality 2 consists of most of the occipital region and part of the basicranium. The bone is stained light brown on the surface, but has a rather chalky appearance inside. It may be of Pleistocene to Recent age. NMC 25183 from Dawson Locality 16 is the dorsal part of a braincase consisting of most of the frontal and parietal bones to which proximal parts of both antlers are attached. Presumably the caribou represented by the fossil died in late summer or autumn near Dawson. The largest of the two pedicels measures approximately 39 mm x 34 mm below the burr. Probably a male in early adulthood is represented. The fossil is tan.

NMC 17400 from Sixtymile Locality 1 was collected by H.S. Bostock in 1933. It consists of the posterior

part of the frontals with the stubs of large antlers attached, the parietals, and the upper half of the occipital region. The largest pedicel below the burr measures approximately 60 mm x 52 mm. The surface of the specimen is highly oxidized. It and NMC 25179 are the largest cranial fragments in the collection.

NMC 11645 from Dawson Locality 32 consists of the right temporal region and a portion of the right frontal of a braincase with the proximal half of an antler attached. The small size of the antler, which lacks a brow tine, but possesses the stub of the bez tine, indicates that the fossil was derived from a female, and further that it had probably died near Dawson between October and May. The pedicel below the burr measures 25 mm x 23 mm. A 170 mm segment of beam is preserved.

NMC 14016 from Old Crow Locality 2 consists of central and left parts of the basicranial region. It is stained deep, reddish brown. NMC 27807 from Old Crow Locality 83 consists of the occipital condyle, the posterior half of the basioccipital, and some surrounding bone. It is gray with rusty brown patches.

NMC 25968 from Dawson Locality 29 is the upper part of a braincase with antler pedicels. The maximum

diameter of the antler scars is 36 mm. An interesting feature of the specimen is that much of its surface, which is tan in color, is covered by a thick layer of gray siltstone that may be of volcanic origin. A cursory examination revealed what appear to be small shards of volcanic glass in the ground mass. It may offer the possibility of a check between a radiocarbon date on bone collagen and an age estimate derived from analysis of the glass shards. NMC 13620 from Old Crow Locality 11A is another frontlet bearing pedicels with antler scars reaching a maximum diameter of 42 mm. It represents a male. This small fragment of bone is relatively heavy and is stained black. It is probably of pre- late Wisconsin age.

Eleven mandibular fragments are described. In most cases the mandibular bone is brown, as is the dentine exposed on the occlusal surfaces of the teeth. The fossils range in age from juvenile to very old. Estimates of the chronological ages of the caribou represented by these fossil mandibles with teeth are based on Miller's (1974, Plates A, B) carefully calibrated chronological series, including mandibles with teeth from one quarter month to 17 years of age. His data are derived from a study of mandibles from more than 900

individuals of both sexes of barren-ground caribou (*Rangifer tarandus groenlandicus*) belonging to the Kaminuriak population, which ranges from northern Manitoba and Saskatchewan to southeastern Keewatin in the Northwest Territories.

Referred left mandibles - NMC 28739 from Old Crow Locality 4 is a complete mandible except for bone anterior to the mental foramen. dLP₂-dLP₄ are present, and LM₁ has started to erupt. I estimate that the specimen represents a 2-month-old calf. The mandibular bone is stained reddish brown. NMC 26976 from Old Crow Locality 22 is the posterior part of a mandible with slightly worn dLP₂-dLP₄. LM₁ has erupted and part of LM₂ can be seen through a break in the bone posterior to LM₁. I estimate that this fossil represents a 3-month-old calf. The diastema and bone on the inferior margin of the mandible (below dLP₂-dLP₄) are lacking. NMC 28737 from Old Crow Locality 11 has LP₂-LM₁ and partial alveoli for LM₂-LM₃. The mandible lacks bone anterior to the mental foramen and posterior to the alveolus for LM₃. The teeth present are well worn, and I estimate that a 5-year-old caribou is represented.

Referred right mandibles - NMC 13607 from Old

Crow Locality 11A is a mandible lacking the anterior tip and bone posterior to RM_2 . dRP_2 - dRP_4 are well worn. RM_1 and the alveolus for RM_2 are present. I estimate that the mandible was derived from a 17-month-old caribou. NMC 26591 from Old Crow Locality 11A is a mandible lacking the anterior tip and bone posterior to RM_3 . dRP_2 is lost and both dRP_3 and dRP_4 are heavily worn. RM_1 and RM_2 are moderately and slightly worn, respectively. RM_3 has erupted and its unworn crests are approximately 5 mm above the alveolar margin. I estimate that the specimen represents an animal that is nearly 2 years old (more precisely 22 months). NMC 14991 from Old Crow Locality 59 is a mandibular fragment with the anterior root and posterior cusp of RP_4 , and RM_1 - RM_3 . The anterolingual portion of RM_3 is broken and occlusal wear on its posterior cusps is slight. I estimate that the specimen represents a 4-year-old animal. NMC 17083 from Old Crow Locality 8 consists of most of a mandible except for the anterior tip and bone posterior to RM_3 . The roots of RM_1 , part of the posterior cusp of RM_2 , and the alveoli for the remaining cheek teeth are present. I estimate that it is from an approximately 4-year-old animal. The bone is tan - more like late Wisconsin bone from Old Crow and Dawson areas than the evidently older more deeply stained bone from those regions.

NMC 14339 from Old Crow Locality 14N consists of a mandible lacking the anterior tip and the ascending ramus above the level of the cheek teeth. The teeth comprise moderately worn RP_2 - RM_3 . I estimate that the caribou that this specimen represents was 6 years old. NMC 29050 from Dawson Locality 30 is the central part of a mandible with heavily worn RP_2 - RM_3 . The teeth are slightly chipped. The small size of the loops on RM_1 indicates that the animal from which the fossil was derived had reached an age of approximately 14 years. NMC 22889 from Old Crow Locality 11A is a mandible with heavily worn RP_3 - RM_2 , and partial alveoli for RP_2 and RM_3 . The lateral surface is pitted, perhaps by acids in the groundwater. I estimate that the caribou represented by this specimen was about 15 years old at death. The loops on RM_1 have been almost completely worn away.

As mentioned previously with respect to horses, metapodials provide an insight into the size of mammals. Only complete metacarpals and metatarsals of Yukon Pleistocene caribou are described.

Referred left metacarpals - NMC 15356 from Old Crow Locality 14N seems to have been gouged and pitted by carnivore teeth on the proximal quarter of the

shaft. It is stained dark brown.

Referred right metacarpals - NMC 26690 from Old Crow Locality 27W is stained blackish brown. NMC 14698 from Old Crow Locality 28 is dark reddish brown. It closely matches a metacarpal of a Recent female from Alaska (NMC 32207). NMC 15268 from Old Crow Locality 22 is split in the upper part of the shaft and eroded on the posterior surface of the distal articulation. It is stained brown. NMC 29126 from Sixtymile Locality 3 is light tan and relatively fresh in appearance. NMC 26774 from Old Crow Locality 20 apparently bears tooth marks of a medium-sized carnivore that cross the length of the shaft. It is stained dark brown. NMC 29125 from Sixtymile Locality 3 is light tan and has fine rootlet impressions on its anterior surface. Pyrolusite "stars" are seen on the surface. A chip of bone is missing from the anteromedial part of the shaft. NMC 25242 from Dawson Locality 2 is light tan, and like NMC 29125 and 29126, is probably of late Wisconsin age.

Referred left metatarsals - NMC 13537 from Dawson Locality 32 lacks bone on both sides near the centre of the shaft. A fine pattern of rootlet impressions covers

the surface, possibly indicating that the caribou represented died in a grassland environment. The bone is dark tan. NMC 29251 from an unknown locality in the Old Crow Basin is small and slender compared to NMC 13537. The upper half of the shaft is badly split. It is stained dark brown.

Referred right metatarsals - NMC 14950 from Eagle Locality 37, although larger than any other Yukon Pleistocene metatarsals collected, is slightly smaller than the metatarsal of a Recent female from Alaska (NMC 32213). It is stained dark brown. NMC 17248 from Dawson Locality 28 is damaged on the lateral side near the proximal end of the shaft, and is cracked. It is light tan. The fossil metatarsals lie within the range of Recent caribou metatarsals from Alaska and the Northwest Territories.

Discussion

Caribou remains have been recorded from many localities throughout the unglaciated Yukon Territory, such as Dawson, Sixtymile, Old Crow, Porcupine River, Eagle River and Peel Plateau. They range in age from pre- late Wisconsin to postglacial. I have excavated specimens *in situ* from the organic subunit of the basal clay at Old Crow Localities 11 and 12, which may be of late

Illinoian age, and from Unit 2 at Old Crow Locality 44, which may be of Sangamon interglacial age (>54,000 years B.P.). Radiocarbon dates on caribou bone vary in age from mid-Wisconsin to postglacial. Radiocarbon analysis of bone from a fleshing tool made of a caribou tibia from Old Crow Locality 14N yielded a date of $27,000 \pm \begin{matrix} 3,000 \\ 2,000 \end{matrix}$ years B.P. (GX-1640). This specimen has been discussed previously under the genus *Homo*. An antler from Dawson Locality 16 yielded a date of $23,900 \pm 470$ years B.P. (I-8580), indicating that caribou were isolated in Eastern Beringia during the peak of the Wisconsin glaciation. Radiocarbon dates of $6,450 \pm 135$ years B.P. (I-4221) and $5,010 \pm 100$ years B.P. (I-8642) on an antler from Old Crow Locality 69 and a radio-ulna from Dawson Locality 8, respectively, indicate that caribou were in the Old Crow and Dawson areas during the warmest part (hypsihermal) of the postglacial. Mackay, *et al.* (1961, p. 34) mention a radiocarbon date of 3,250 years B.P. (P-228) on a caribou antler from the lower fossiliferous layer at Engigstciak near the arctic coast of the Yukon.

In other parts of Canada, caribou fossils have been reported from: gravels 3 feet (0.9 m) above bedrock and 165 feet (50.3 m) below the surface at Wingdam, British Columbia (Cowan 1941, p. 43), in what I consider

may be interglacial deposits of Sangamon age or earlier - the specimen may represent a taxon other than *Rangifer tarandus*; Sangamon interglacial deposits at Medicine Hat, Alberta (Stalker and Churcher 1970); late Wisconsin gravels at Cochrane, Alberta. Fossils from these gravels have yielded radiocarbon dates of approximately 11,000 years B.P. (Churcher 1968, p. 1470); late Wisconsin to postglacial deposits near Toronto (e.g. Carleton Bar, Taylor's Brickyard), Ontario (Coleman 1899, p. 195; Hay 1923, p. 244); late Pleistocene to postglacial deposits in the Northwest Territories: e.g. Baillie Islands; Masik River, Banks Island; raised beaches of probable postglacial age near Alert, Ellesmere Island; postglacial (approximately 5,000 years old) deposits at Great Bear River; and Acasta Lake and Grant Lake (approximately 7,000 years old) (Banfield 1961, p. 34; Harington 1971a, pp. 82-83; Harington 1976 MS., pp. 49, 53).

In the conterminous United States, caribou remains are known from: Idaho, Iowa, Minnesota, Wisconsin, Illinois, Kentucky, Michigan, Tennessee, Virginia, Pennsylvania, New Jersey, New York, Vermont, Connecticut, Massachusetts, and Ohio (Anderson and White 1975, p. 63). Evidently a *Rangifer*-like form - possibly related to the "first group" (Cervidae - genera and species undetermined)

of deer from the Yukon Pleistocene - occupied South Dakota during Nebraskan or Kansan time (Green and Lillegraven 1965, p. 48). Three records from Sullivan County, Tennessee (Guy Wilson, Beartown, and Baker Bluff caves), mark the southernmost known limits of caribou in North America. They lie some 200 miles (322 km) southeast of the Wisconsin terminal moraine in Ohio, and 800 miles (1,287 km) south of the known historic range of *Rangifer tarandus* in North America. Radiocarbon dates associated with caribou in the conterminous United States are: 19,700 \pm 600 years B.P. (I-4163) from Guy Wilson Cave, Tennessee; 13,460 \pm 420 years B.P. (SI-461) from Saltville, Virginia; 12,530 \pm 370 years B.P. (I-4137) from Dutchess Quarry, New York; 10,370 \pm 350 years B.P. from Jaguar Cave, Idaho (Guilday and Hamilton 1975, p. 111; Kurtén and Anderson 1972, Table 16). These dates support the occurrence of caribou herds well south of the North American continental ice mass during the peak of the Wisconsin glaciation.

In Alaska, the earliest record of caribou ("*Rangifer* sp.") is rather insecure. The identification is based solely on a heavily worn dP³ from Cape Deceit (?Nebraskan) (Guthrie and Matthews 1971, Figure 10). The pelvis of a deer, "probably *Rangifer*", found in a

gully in the coastal bluffs of Baldwin Peninsula, Kotzebue Sound, may have been derived from beds dating to the time of the Kotzebuan marine transgression (?Yarmouth interglacial) (Péwé and Hopkins 1967, pp. 268-269, footnote C). Caribou fossils have been collected from Illinoian deposits at Cripple Creek Sump and Gold Hill near Fairbanks (Péwé 1975a, Table 11). *Rangifer tarandus* has also been reported from Wisconsin sediments at Fairbanks and Engineer creeks in the same area (Guthrie 1968b, Table 1). Remains of what may be caribou ("Cervidae cf. *Rangifer*") are known from late Pleistocene sediments at Tofty (Repenning *et al.* 1964, Table 1). Repenning (Weber 1975, p. 67) has identified "caribou(?)" bones from late Pleistocene stream channel fill at Canyon Creek near Big Delta. I (Harrington 1976 MS., pp. 75, 78) have identified late Pleistocene *Rangifer tarandus* fossils from the Kuk and Ikpihpuk rivers near the arctic coast of Alaska, and from late Wisconsin deposits at Lost Chicken Creek in eastern Alaska.

In Siberia, the earliest evidence is "*Rangifer* sp." from the Olyor Suite of ?Kansan age (Sher 1971, p. 89). *Rangifer tarandus* is reported from: the Riss II (late Illinoian) Utka Beds on the Maly Anyui River; late Pleistocene (Illinoian to Wisconsin) deposits of Bolshoi

Lyakhov Island (Vangengeim 1961); the early Wisconsin Iedoma Suite on the Kolyma River; the late Wisconsin Alioshka Suite on the Kolyma River, and many other sites of late Wisconsin or early postglacial age (e.g. Proliv Dmitriya Lapteva, and the Berelekh River (radiocarbon dated at $12,240 \pm 160$ years B.P.)) (Vereshchagin 1974).

The earliest known record of *Rangifer tarandus* in Europe is from Günz II (?late Nebraskan) sands at Süssenborn, Germany. Caribou occur next in Mindel (?Kansan) deposits at Mosbach, Bad Frankenhausen, and Steinheim. The species is also known from sediments of Riss (Illinoian) age. During the Würm (Wisconsin) glaciation it ranged widely throughout Europe from Spain and Italy to the southern USSR (Kurtén 1968, p. 170). Remains are particularly abundant in Magdalenian deposits, which span the period from approximately 15,000 to 10,000 years B.P. (Ucko and Rosenfeld 1967, p. 31), when it was the main prey of many groups of early human hunters.

Banfield (1974, p. 383) gives several anatomical reasons for considering *Rangifer* to be an extremely primitive deer. Despite this evidence, the ancestry of the genus is not known. I would, however, point out the

remarkable similarity in the appearance of the antlers of "*Cervus savini*" (e.g. BM(NH) M 6093, M 17179) from the Forest Bed of Trimingham near Norfolk, England, and those of *Rangifer tarandus*. Although "*Cervus savini*" is probably somewhat later in age than caribou fossils from Süssenborn, I speculate that this deer had Villafranchian ancestors in southern Europe, which were related to the *Euctenoceros* stock. The possibility of parallel evolution of similar antler forms complicates the problem of tracing the evolution of taxa such as *Rangifer* where early fossil evidence is scarce.

I suggest that the boreal forest-adapted woodland caribou with its relatively heavy, laterally compressed antler beams would most closely approach the ancestral form. When the expansion of cool steppe grasslands and tundra occurred near the beginning of the Pleistocene, presumably this ancestral form, which may have adapted to feeding on arboreal lichens, would have the basic adaptation necessary for exploiting new arctic and alpine tundra habitats that offered an abundance of ground and rock lichens. Considering the openness of this fresh terrain, it is reasonable to expect that larger antlers like those of the barren-ground caribou would be developed; they would probably be advantageous from a

viewpoint of social behavior.

In summary, *Rangifer* may have evolved in Beringia, or in boreal areas to the south of it, and spread widely across cool, tundra-like terrain of the Holarctic from Alaska (Cape Deceit) to Europe (Süssenborn) in Nebraskan time. It is known from northeastern Siberia (Kolyma River) and Europe during the Kansan glaciation, but, surprisingly, does not appear to be certainly represented from North American then. *Rangifer tarandus* is known from Illinoian deposits of Alaska (Fairbanks) and possibly Illinoian sediments in the Yukon (Old Crow), and was well established from western Europe to northeastern Siberia during that glaciation. The species first seems to have reached central North America (Medicine Hat) during the Sangamon interglacial. By the time the Wisconsin ice sheet had reached its maximum extent caribou occupied a thin, possibly discontinuous, belt of tundra-like terrain and boreal forest from Idaho to Tennessee (the southern limit). Caribou were abundant in Eastern Beringia during the late Wisconsin. At that time in Eurasia, caribou were common in Siberia and had reached the southern European limits of their range in Italy and Spain. They began shifting northward to Scandinavia during the Mesolithic period. Herds existed in the northwestern United States

(Jaguar Cave) and on the edge of the southwestern Canadian prairies about 10,000 to 11,000 years ago, while in eastern North America, evidently caribou had retreated northward to New York by about 12,500 years ago (Dutchess Quarry).

At least some caribou occupying the western part of the southern refugium were of the graceful-antlered barren-ground form (e.g. ISUM 23114), while some in the east were of the woodland form (e.g. CM 12603) (Guilday 1966, p. 325). Therefore, in an attempt to explain the distribution of Recent subspecies, I suggest the following scheme: (a) during the retreat of the late Wisconsin ice herds of barren-ground caribou (*Rangifer tarandus groenlandicus*) from Minnesota to Idaho moved northward into the northern Cordillera, Keewatin, and across sea ice to Baffin Island and southwest Greenland (probably reinvading the area from which their ancestors had been displaced) by about 7,000 years ago (Acasta Lake) or later; (b) that woodland caribou (*Rangifer tarandus caribou*) concentrated in the northeastern United States retreated to their present range in Quebec and Newfoundland, and also spread northwestward into the broadening boreal forest as it shifted to the north, the barren-ground

caribou having moved north ahead of the woodland animals; (c) that small tundra caribou or Peary caribou (*Rangifer tarandus pearyi*), having been isolated in unglaciated western Banks Island, spread eastward across the sea ice to occupy most of the Canadian Arctic Islands; (d) that small Greenland caribou (*Rangifer tarandus eogroenlandicus*), derived from a similar stock to the Peary caribou, survived the Wisconsin glaciation in the Pearyland refugium, spreading south along the east coast during the postglacial, where they recently became extinct; (e) that Grant's caribou (*Rangifer tarandus granti*), which subspeciated in Eastern Beringia, remained for the most part in that region, possibly with some intergradation with *Rangifer tarandus groenlandicus* to the east and *Rangifer tarandus caribou* to the south (Youngman 1975, pp. 163, 166); and (f) that Dawson's caribou (*Rangifer tarandus dawsoni*) became isolated from other herds of the woodland type on the British Columbia mainland and survived the Wisconsin glaciation in impoverished range on the Queen Charlotte Islands, where they became extinct about 1936.

Caribou or reindeer (*Rangifer tarandus*) occur in a broad belt of tundra and bordering boreal forest from Scandinavia to Siberia and across North America

from Alaska to Greenland and Newfoundland. In the Yukon Territory, woodland caribou (*Rangifer tarandus caribou*) are found in the southern half, while Grant's caribou (*Rangifer tarandus granti*), which are most closely related to the tundra form (*Rangifer tarandus groenlandicus*), dominate the northern half. Occasionally, Peary caribou (*Rangifer tarandus pearyi*) may reach the northern Yukon (Youngman 1975, p. 163).

Caribou are small to medium-sized deer characterized by chunky, well-furred bodies, large blunt muzzles, short ears and tails, large hooves and semipalmate antlers that generally sweep back, out and then forward, having two main proximal tines (brow and bez) which branch off close to the burr, and other distal tines. Unlike most deer, female caribou usually bear antlers, albeit short and spindly ones compared to those of males. Since antlers of females and subadults are smaller and weaker, they are less likely to be preserved; therefore, most Pleistocene caribou antlers found are those of adult males. In adult males, antler growth begins in March, and by October when rutting begins, they are several feet long and polished clean of velvet. Antlers are dropped in winter, beginning in November. Antlers of adult females develop from June to September, are polished clean of velvet in late October, and are dropped

during calving in April or May. Caribou antlers are notoriously variable within populations (Kelsall 1968, p. 38), making identification of fossil antler fragments of caribou or related taxa by paleontologists a hazardous task.

Caribou are gregarious, generally occurring in bands of 10 to 50, or in loose herds of up to a thousand animals. They become concentrated at three periods: (a) in late winter before the spring migration; (b) after calving; and (c) during the rutting period before the autumn migration. They can travel rapidly and swim well, buoyed up by their thick coats. Barren-ground caribou move up to 800 miles (1,287 km) between summer tundra range and winter range on the margin of the boreal forest. Mountain and woodland caribou, like wapiti, tend to migrate from higher summer range to lower winter range.

Caribou occupy arctic and alpine tundra, subarctic taiga, and boreal and subalpine forest. As almost all of the caribou antlers from Yukon Pleistocene deposits are of the barren-ground type, presumably they are indicative of broad areas of tundra-like terrain, and perhaps some zones of boreal or subalpine forest in Eastern Beringia during the late Pleistocene. Fossil antler fragments (keeping in mind their variability) suggest that woodland caribou rarely

lived in the Dawson and Old Crow areas during the late Pleistocene. Caribou are well adapted to cold conditions, by their thick, well-insulated coats, blunt, heavily-furred muzzles, short furry ears and tails and large hooves (which aid their movement over snow, and which develop so that the pads are insulated in winter).

Lichens are the main food of caribou - particularly in winter. They eat about 10 pounds (4.5 kg) of lichens per day. Other winter foods are horsetails, sedges, and willow and birch twigs. Summer diet includes mushrooms, lichens, grasses, sedges, forbs, and willow and birch twigs and leaves.

Man is one of the main predators of caribou. Archeological evidence from Old Crow and Dawson areas indicates that people likely hunted caribou there during the mid- to late Wisconsin. Archeologists have shown, or have given good reasons for inferring, that caribou were important prey of Paleo-Indians in eastern North America during the late Wisconsin. In the west, caribou remains have been found in middens approximately 10,300 years old at Jaguar Cave, Idaho. Likely, caribou were hunted at Acasta and Grant lakes, Northwest Territories about 7,000 years ago by hunters that had moved northward with the retreating

Wisconsin ice (Harrington 1976 MS., pp. 95-96). Apart from man, wolves are the most serious predator of caribou. They generally kill young, old or disabled animals. Brown bears, wolverines and lynx occasionally kill caribou. According to Banfield (1974, p. 386), eagles are important predators of new-born calves.

Cervidae (genera and species undetermined)

In the collection of antler remains from Yukon Pleistocene deposits are two groups of cervid specimens that neither correspond to typical barren-ground caribou nor wapiti antlers. They have in common laterally compressed beams, and both have some characteristics of woodland caribou antlers, but I am not sure that they are referable to *Rangifer tarandus* or even *Rangifer*. Until the evidence is clearer, these groups will be considered as belonging to undetermined genera and species of deer (Figure 75A-D, Table 85).

Referred specimens

The first group consists of seven antler fragments that have the following characteristics: (a) beams that are oval (anteroposteriorly longer) to round in cross section at the burr; (b) beams that gradually become laterally compressed, and which tend to spread

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Figure 75. Proximal portion of an unshed right antler (NMC 14338, Old Crow Locality 14N) of a Pleistocene cervid (genus and species undetermined - "First Group").

A. Medial view.

B. Anterior view.

Fragment of a shed right antler (NMC 29139, Sixtymile Locality 3) of a Pleistocene cervid (genus and species undetermined - "Second Group").

C. Medial view

D. Anterior view.

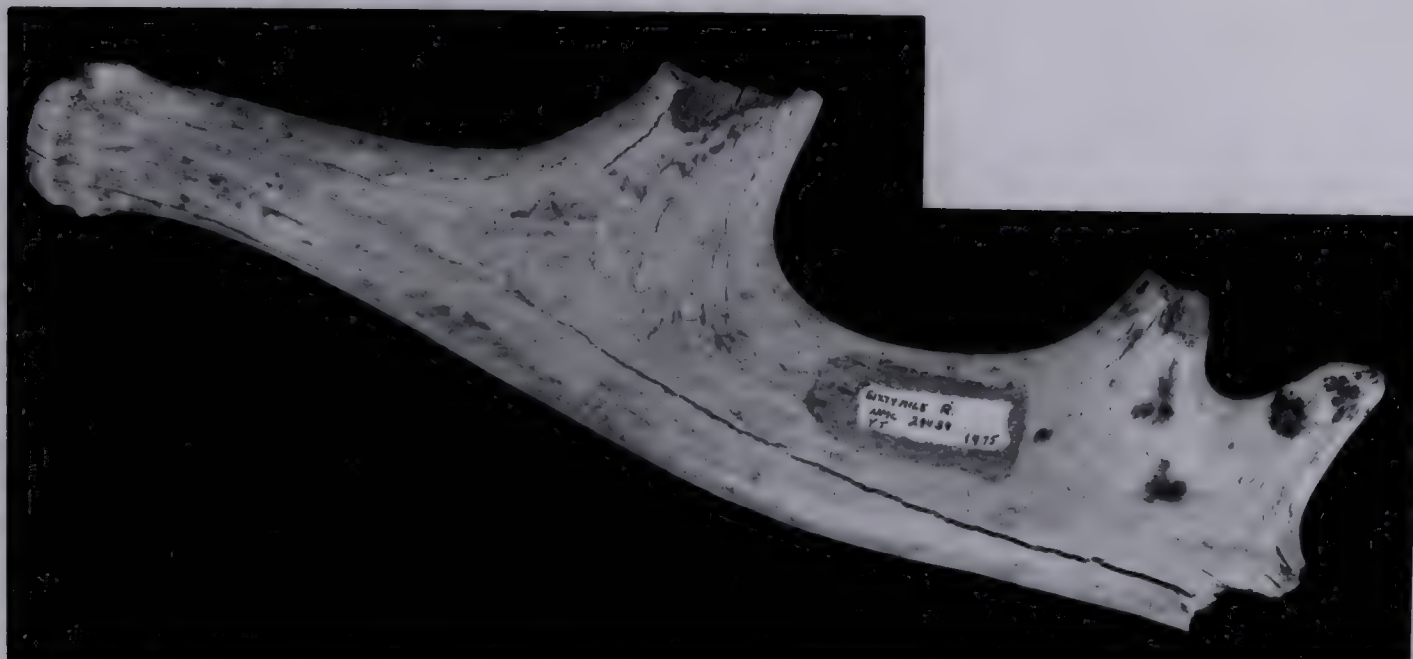
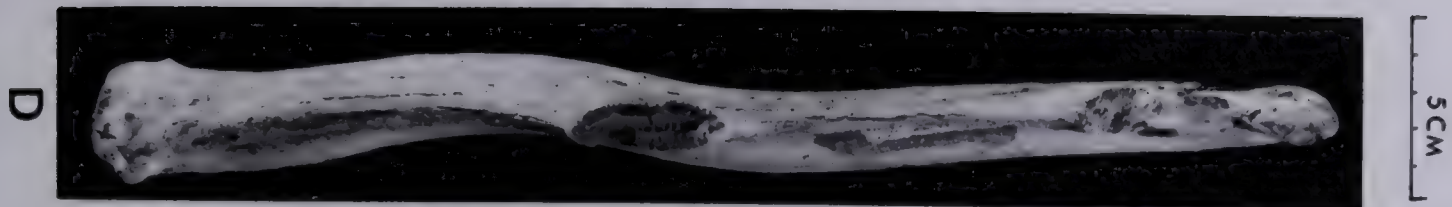


Table 85. Measurements of Pleistocene cervid (genera and species undetermined) antlers from the Yukon Territory.

Specimens	Measurements (mm)*							
	1	2	3	4	5	6	7	8
Cervidae (genus and species undetermined)								
First Group.								
NMC 27841 Old Crow Loc. 67	-	45.3	53.9	41.9	55.0	37.5	72.0	36.4
NMC 20917 Old Crow Loc. 29	49.7	40.8	48.7	37.8	48.3	37.1	50.2	35.4
NMC 13619 Old Crow Loc. 11A	52.2	48.8	45.4	36.8	46.6	35.5	53.9	32.9
NMC 23371 Old Crow Loc. 42	44.9	44.1	46.8	41.9	51.2	40.2	60.5e	40.3e
NMC 14338 Old Crow Loc. 14N	46.8	44.0	48.3	35.0	58.5	32.5	81.5	33.5
NMC 24181 Old Crow Loc. 3 (immature?)	29.6	26.6	38.0	22.2	46.6e	19.0	-	-
NMC 14760 Old Crow Loc. 29 (immature?)	29.8	25.3	33.2	17.2	-	-	-	-
Second Group.								
NMC 29139 Sixtymile Loc. 3	32.4	29.8	36.1	26.3	52.6	22.6	-	-
NMC 27999 Old Crow Loc. 95	27.7	22.6	35.8	18.3	38.3	17.3	44.2	15.7
NMC 28202 Old Crow Loc. 116	35.7	31.0	51.7a	25.4a	53.4	24.4	-	-

* 1 - Anteroposterior diameter of antler base (or pedicel below burr, if antler is attached to cranium).

2 - Mediolateral diameter of antler base (or pedicel below burr, if antler is attached to cranium).

3 - Minimum anteroposterior diameter of beam 50 mm above burr.

4 - Minimum mediolateral diameter of beam 50 mm above burr.

5 - Minimum anteroposterior diameter of beam 100 mm above burr.

6 - Minimum mediolateral diameter of beam 100 mm above burr.

7 - Minimum anteroposterior diameter of beam 175 mm above burr.

8 - Minimum mediolateral diameter of beam 175 mm above burr.

anteroposteriorly as the distance from the burr increases; (c) beams that are generally teardrop-shaped (widest part posterior), or rarely elliptical (anteroposteriorly longer) in cross section half way between the burr and the second anterior tine (where it is preserved); (d) brow projections apparently varying from single, well developed tines, to twin, stubby projections - the medial one being directed slightly inward toward the mid-line of the cranium, the lateral one projecting forward; to a single nubbin directed slightly inward in the smaller antlers assigned to this group; (e) brow projections located close to or arising directly from the burr - the position of brow tines in *Rangifer* and *Dama*; (f) antler beams showing only faint signs of longitudinally oriented vascular grooves; more like the vascular impressions in caribou, than the deep vascular grooves in wapiti; (g) adult male antlers with second anterior tines generally developing approximately 180 mm or more distal to the burr; (h) antlers which appear to rise high from the frontal plane, more like those of wapiti than barren-ground caribou antlers I have seen which tend to sweep back sharply, almost in the plane of the frontals, before curving forward. The largest antler fragments, which I consider represent adult males, suggest that this group of deer is large - perhaps reaching woodland caribou or nearly wapiti size when mature.

I know of no living or fossil American deer that have antlers with the above characteristics. Two late Pleistocene cervids, *Navahoceros fricki* (Wyoming, New Mexico, Mexico) and *Sangamona whitneyi* (Iowa, Illinois, Tennessee), should be considered in this respect. Kurtén (personal communication 1976) states that the former has simply-built forked antlers, and the antlers of the latter are not known. These genera must be described and illustrated in more detail before any decision can be made concerning their relationship, if any, with the undetermined Yukon Pleistocene deer.

Two fossils from deposits of pre- Wisconsin age that have previously been described as belonging to caribou, but that appear to have characteristics of the first group of Yukon cervids, are worth noting. BCPM 696 from Wingdam, British Columbia, described as the right antler of a female of "*Rangifer* sp." by Cowan (1941, p. 43, Plate II, Figure 2), has a brow tine projecting forward at the level of the burr, a compressed antero-posteriorly spreading beam below the second anterior tine, and a second anterior tine widely separated from the brow tine (as in NMC 27841 and 13619 from the Yukon). Unfortunately no measurements are provided for this fossil, and there is no scale on the photograph of it.

I consider that this specimen is of Sangamon or earlier interglacial age. SDSM 6421 from gravels of the Herrick Formation (?Nebraskan or Kansan) is a small fragment of antler attached to a cranial fragment. The antler has a low brow tine and a robust, laterally compressed beam like the Yukon fossils of the first group. The fossil was found with *Equus (Plesippus)* sp. and *Stegomastodon mirificus*. I am not sure that it is referable to a woodland caribou as Green and Lillegraven (1965, p. 48) suggest.

Among living deer of Eurasia of which I am aware, the Yukon antlers are closest in conformation to those of fallow deer (*Dama* sp.), which Cornwall (1964, p. 69) characterizes as follows: "The antler is very smooth and the marks of the blood-vessels shallow {i.e. faint vascular grooves}. The brow tine springs from the beam directly above, almost in contact with the burr. A bezel tine is generally absent and the antler tends to be markedly palmated above the trez." Unfortunately, no *Dama* antlers are available for comparison. Evidently the Yukon deer antlers of the first group differ from those of *Dama dama* in that a large brow tine was not always present, and I am not sure how the distal parts of the Yukon fossil antlers would compare, for they are not preserved. Among remains of extinct Eurasian deer, the

Yukon fossils should be compared to *Euctenoceros tetraceros* antlers (Azzaroli 1953, Figure 15), which, however, appear to have more strongly developed brow tines and more cylindrical beams.

Referred left antlers - NMC 20917 from Old Crow Locality 29 is the proximal part of an antler, the beam of which extends for 290 mm without any indication of a second anterior tine. The brow tine, which seems to have been triangular (apex up) in cross section at the base, has been broken off. The beam is attached to part of the left frontal. The surface of this fossil is deeply oxidized. NMC 23371 from Old Crow Locality 42 is a proximal portion of an antler attached to a small cranial fragment. An 80 mm segment of beam is preserved. Twin stubby projections are located in the brow tine region, originating at the level of the burr. Their centres are 43 mm apart. The lateral one projects forward while the medial one is directed obliquely toward the cranial axis. The leading edge of the antler extends distally from the medial projection. The bone of NMC 23371 is stained dark brown.

Referred right antlers - NMC 27841 from Old Crow Locality 67 is the proximal part of a shed antler. A

large area near the burr, where a brow tine may have been, is missing. A deep, laterally compressed second anterior tine (60 mm x 29 mm) extends 110 mm forward to the point where it was broken. A 280 mm segment of beam is preserved. The surface of the specimen is heavily oxidized. NMC 14338 from Old Crow Locality 14N compares closely with NMC 27841, except that only a 190 mm segment of beam is preserved, a second anterior tine is not evident, and the beam is attached to a small part of the frontal. A triangular scar marks the point where the brow tine has been broken off. This specimen shows the faintness of the longitudinal vascular grooves on the beam. NMC 13619 from Old Crow Locality 11A is an antler beam with twin stubs in place of the brow tine, and part of a laterally compressed second anterior tine. It is attached to a frontal fragment carrying 60 mm of the frontal suture, which enables it to be properly orientated. The antler must have risen at a sharp angle like that of a wapiti, rather than that of a male barren-ground caribou to which it was compared. The slightly eroded twin brow projections are like those of NMC 23371. Their centres are 38 mm apart. The leading edge of the antler beam extends distally from the medial projection. A 240 mm segment of beam is preserved. The fossil is brownish black. Its heavy permineralization

suggests a relatively early geological age. NMC 24181 from Old Crow Locality 3 is an antler fragment with a single, inwardly directed nubbin in place of a brow tine (it may be an incipient brow tine). The antler appears to have been attached to the cranium, but the pedicel-burr region is obscured by heavy erosion. A 103 mm segment of antler beam is present. Perhaps because of the shortness of the beam preserved, there is no indication of a second anterior tine. Probably this fossil represents a young individual. NMC 14760 from Old Crow Locality 29 is a shed antler fragment with an inwardly directed nubbin in place of a brow tine. There is no evidence of a second anterior tine in the 90 mm of beam preserved. A sharp keel occurs distal to the nubbin on the leading edge of the beam. I suggest that this specimen is from a slightly younger animal than NMC 24181. As I envisage this group, successive chronological age classes from young to old may be exemplified by the following sequence: NMC 14760 - NMC 24181 - NMC 13619 - NMC 27841.

The second group is characterized by: (a) relative straightness of the antler when viewed from the front and side; (b) the high degree of lateral compression of the antler, which extends distally to the point where it is

virtually a palmation; (c) brow and bez tines are separated like those of caribou; (d) as in caribou, surface vascular grooving is not deep; (e) relatively small antler bases, which could be related to the fact that the fossils represent female or young animals. Possibly these specimens are parts of aberrant caribou antlers. One of them is reminiscent of the unusual pattern of a stag's antlers in a herd of Quebec caribou (Bergerud 1973, Figure 4).

NMC 29139 from Sixtymile Locality 3 appears to be most of a shed right antler. The brow tine, which was small, is damaged. The second anterior tine is broken 50 mm from its point of origin, and is deep and highly compressed laterally (45 mm deep x 15 mm thick). The third and fourth anterior tines are approximately 45 mm apart. They are poorly developed and laterally compressed. The antler is broken near the tip, which probably extended only a short distance above the fourth anterior tine. There is no indication of a first posterior tine. The relatively thick posterior ridge of the antler forms its main support: it tapers forward creating a thin keel between the projecting tines. A 330 mm segment of beam is preserved. NMC 29139 is similar in some respects to antlers of stag 21 in a herd

of caribou from Mount Albert, Quebec (Bergerud 1973, Figure 4). For example, there are no posterior tines, the main beam rises vertically with a slight backsweep, and there is a tendency to spatulation between the forward projecting tines. NMC 29139 is pale buff, and I suggest that it is of late Wisconsin age.

NMC 27999 from Old Crow Locality 95 is estimated to be the proximal half of a shed left antler. As in NMC 29139, the brow tine is poorly developed (17 mm deep x 13 mm thick), and is separated from the minute, laterally compressed second anterior tine by 90 mm. A damaged first posterior tine or keel occurs approximately 170 mm above the burr. As in the Sixtymile specimen, the main support for the beam is the posterior ridge, the anterior margin being keeled. A 210 mm segment of beam is preserved. The fossil is stained dark brown.

NMC 28202 from Old Crow Locality 116 is a small, laterally compressed basal portion of a shed left antler. It seems to be from an older individual than either NMC 29139 or 27999, being more robust. The burr is well preserved. The stub of the brow tine (26 mm deep x 22 mm thick) and the beginning of a second anterior tine are present. As in other fossils of this

group, the main support for the beam is a posterior ridge that tapers forward to a keel between the tines. A 150 mm segment of beam is preserved. The specimen is stained dark brown.

Discussion

In summary, the antler remains of the first group, unless they are all aberrant caribou antler fragments, seem to represent a large deer that may have lived in the Yukon Territory earlier than most mammals represented in Yukon Pleistocene deposits. So far, specimens are confined to the Old Crow Basin. Antlers of the second group probably represent a smaller cervid more closely allied to *Rangifer*, if indeed they are not aberrant *Rangifer tarandus* antlers. The rather small basal size of these antlers may indicate that they are from young individuals. The staining of the antler fragments suggests that these animals occupied Eastern Beringia during pre-Wisconsin and late Wisconsin time.

Family Bovidae

Bison alaskensis (Alaskan bison)

Two specimens from Yukon Pleistocene deposits are referred to the Alaskan bison (Figure 76A-C, Table 86). This species had larger horns than any other bison known from Eastern Beringia, and may be close to the stock that first arrived in North America from Eurasia.

Before proceeding with a description of the Alaskan bison fossils and a summary of the dispersal history of bison, I wish to point out that my rather conservative use of names such as *Bison alaskensis* and *Bison crassicornis*, rather than *Bison priscus alaskensis* and *Bison priscus crassicornis* (e.g. Flerov 1972, Wilson 1974), is based on a desire to look carefully before leaping. Although the application of *priscus* seems reasonable and appropriate here, I consider that the name should not be formally used until adequate statistical comparisons have been published supporting the relationships between the Eurasian and North American bison in question.

Referred specimens

NMC 13506 from Dawson Locality 33 is an unusually large left horncore with damaged tip and attached cranial fragment (since removed for radiocarbon dating). It was

Figure 76. Left horncore with attached cranial fragment (NMC 13506, Dawson Locality 33) of a Pleistocene Alaskan bison (*Bison alaskensis*). The tip of the horncore is missing.

A. Dorsal view.

B. Posterior view.

C. Ventral view.

Bone from this specimen yielded a radiocarbon date of > 39,900 years B.P. (I-5405).

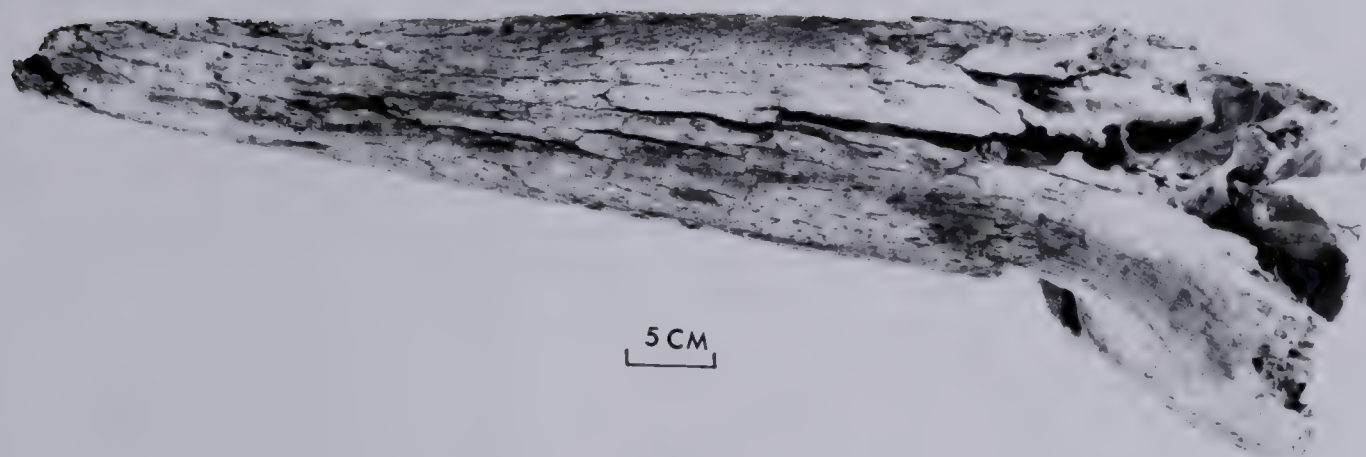
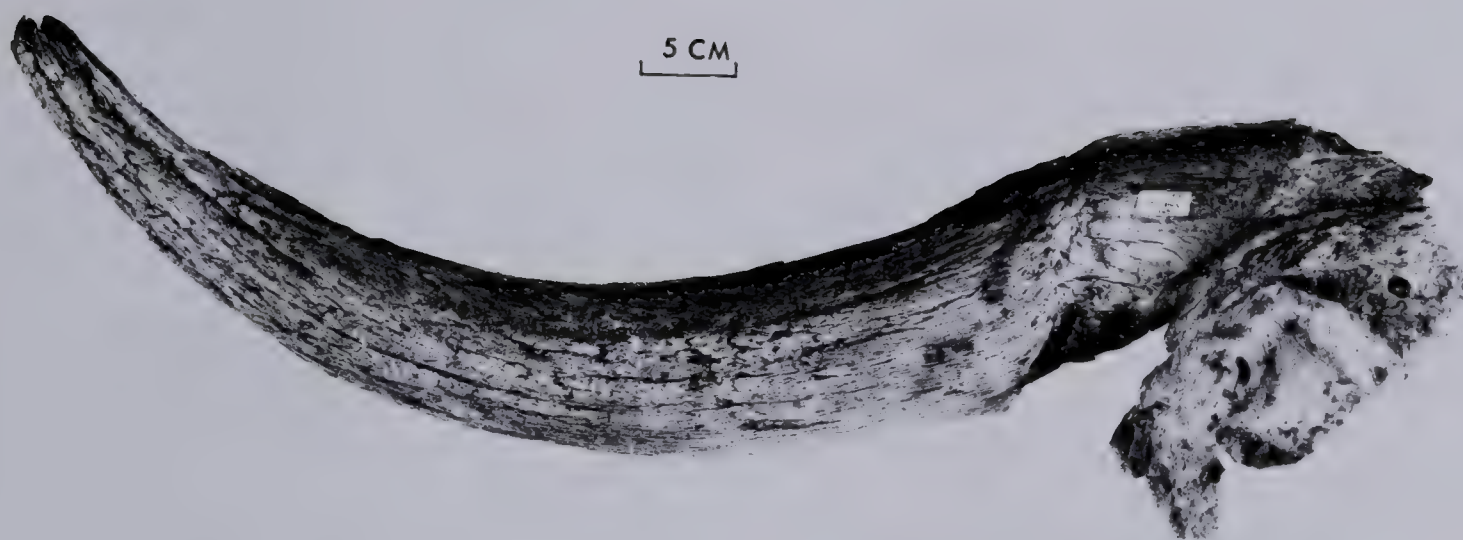
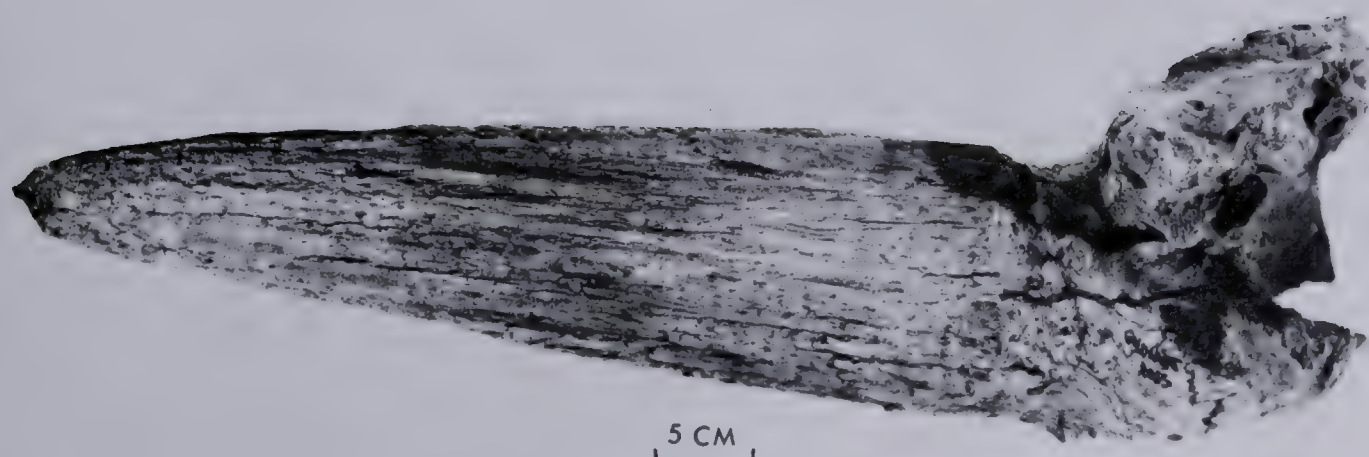
**A****B****C**

Table 86. Measurements of Pleistocene Alaskan bison (*Bison alaskensis*) crania from the Yukon Territory compared to those of Alaskan bison from Alaska, *Bison priscus gigas* from Asia and *Bison crassicornis* and *Bison latifrons* from North America.

SPECIMENS	SEX	ESTIMATED AGE	MEASUREMENTS (mm) *																														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>Bison alaskensis</i> .Pleistocene, Y.T.																																	
NMC 13506 Dawson Loc. 32	♂	Adult	1330e	-	570e	590e	520e	108	135	380	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	113e	80	150	-	
NMC 23349 Old Crow Loc. 96	♂	Adult	1220e	1230e	547e	573e	485e	97	115	339	285	142	81	106	154	310e	308	360	-	-	-	-	-	-	-	-	-	-	267	118e	84	161e	178e
<i>Bison alaskensis</i> .Pleistocene, Alaska (Skinner and Kaisen 1947, Table 18)																																	
CHRM P 25226 Point Barrow area (type)	♂	Adult	1115	1130	475	528	400	95	129	355	311	160	-	-	163	-	339	402	-	-	-	-	-	-	-	-	-	-	307	132	74	134	140
F:AM 46939 Cripple Ck.	♂	Adult	-	-	520	580	465	105	150	425	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	126	70	122	-	
F:AM 46940 Engineer Ck.	♂	Adult	-	-	-	-	-	113	135	402	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	78	-	-	
<i>Bison priscus gigas</i> .Pleistocene, U.S.S.R.**																																	
PIN catalog number unknown	♂	Adult	-	-	603	-	515	99	127	350	-	-	-	-	-	365	301	360	252	-	-	-	-	-	-	-	-	-	-	78	172	200	
<i>Bison crassicornis</i> .Pleistocene, Alaska and Y.T. (Skinner and Kaisen 1947, Table 16)																																	
M	♂♂	Adult	963	986	409	458	365	98	110	324	284	136	-	-	159	-	288	349	-	196	120	147	92	152	523	-	491	272	125	90	126	143	
OR			765- 1295	790- 1322	295- 610	310- 650	280- 530	82- 118	90- 137	272- 388	250- 314	115- 159	-	-	141- 185	-	255- 332	307- 408	-	177- 213	112- 131	131- 166	72- 115	137- 161	487- 560	-	473- 503	235- 315	107- 153	81- 103	100- 166	110- 189	
N			118	108	208	207	207	207	291	286	131	150	-	-	153	-	156	110	-	21	7	37	30	8	8	-	10	107	207	157	115	113	
<i>Bison latifrons</i> .Pleistocene, Conterminous U.S. and Mexico (Skinner and Kaisen 1947, Table 19)																																	
M	♂♂	Adult	1758	1724	830	934	810	144	162	481	323	157	-	-	176	-	370	397	-	219	126	162	104	177	577	-	-	306	118	89	176	245	
OR			1422- 2129	1560- 1945	650- 1115	800- 1156	180- 1020	123- 164	140- 184	420- 546	306- 340	140- 175	-	-	151- 188	-	348- 402	357- 434	-	218- 220	-	-	97- 110	-	574- 580	-	-	301- 310	110- 131	80- 93	147- 210	209- 300	
N			10	6	12	9	8	15	15	16	6	8	-	-	7	-	10	4	-	2	1	1	2	1	2	-	-	2	8	15	10	6	

*1 - Spread of horncores (tip to tip).

2 - Greatest spread of horncores (on outside curve).

3 - Horncore length on upper curve (tip to burr).

4 - Horncore length on lower curve (tip to burr).

5 - Length (tip of horncore to upper centre of burr).

6 - Vertical diameter of horncore (at right angle to longitudinal axis).

7 - Transverse diameter of horncore (at right angle to longitudinal axis).

8 - Horncore circumference (at right angle to longitudinal axis).

9 - Greatest width (at auditory openings).

10 - Width across occipital condyles (disregarding occasional anterolateral expansions of occipital condylar bone).

11 - Basioccipital width (across posterolateral margins).

12 - Cranial depth (highest point of occipital crest to top of foramen magnum).

13 - Cranial depth (occipital crest to lower border of foramen magnum).

14 - Cranial width (between upper centres of horncore burrs).

15 - Cranial width (constriction between horncores and orbits).

16 - Greatest postorbital width.

17 - Anterior orbital width (at notch).

18 - Width (at masseteric processes above M¹).

19 - Rostral width (at maxillary - premaxillary suture above P²).

20 - Alveolar length (P²-M³).

21 - Alveolar length(M¹-M³).

22 -Length (anterior alveolar margin of P² to tip of premaxilla).

23 - Basal length (lower lip of foramen magnum to tip of premaxilla).

24 - Condylbasal length (posterior border of occipital condyles to tip of premaxilla).

25 - Length (occipital crest to tip of nasals).

26 - Posterianal length (occipital crest to nasofrontal suture).

27 - Index of horncore curvature ($\frac{\text{measurement 4}}{\text{measurement 5}} \times 100$).

28 - Index of horncore compression ($\frac{\text{measurement 6}}{\text{measurement 7}} \times 100$).

29 - Index of horncore proportion ($\frac{\text{measurement 3}}{\text{measurement 8}} \times 100$).

30 - Index of horncore length ($\frac{\text{measurement 3}}{\text{measurement 15}} \times 100$).

NB - Most measurements follow those of Skinner and Kaisen (1947, pp. 142-145), but many of the numbers designating them have been altered. Some new measurements have been added and earlier ones have been omitted for practical purposes.

** I am grateful to K.K. Flerov for allowing me to take measurements on a cranium of *Bison priscus gigas*, which is on display in the Paleontological Institute of the Academy of Sciences of the U.S.S.R., Moscow.

recovered by L. Ross while placer mining on Gold Run Creek in the summer of 1968. It came from a depth of approximately 45 feet (13.7 m) below the surface. It is of larger grade than all other Yukon bison cranial specimens which I have examined, except for NMC 23349. Among described type specimens of bison, NMC 13506 approaches most closely *Bison alaskensis* (CNHM P 25226) from the Point Barrow area, Alaska, which was described by Rhoads in 1897. Similarities include: (a) relative straightness of the horncore when viewed from above; (b) the high degree of dorsoventral compression near the base of the horncore; and (c) great length. In tip to tip spread of the horncores, I estimate that NMC 13506 is greater than the type of *Bison alaskensis*, beyond the range for *Bison crassicornis*, and below the range for *Bison latifrons*. It is closer in size to two specimens (F:AM 46939 and 46940) from near Fairbanks that Skinner and Kaisen (1947, pp. 201, 203) have referred to *Bison alaskensis*.

NMC 23349 from Old Crow Locality 96 is a posterior cranial fragment with horncores. I estimate that the left horncore lacks approximately 70 mm at the tip, and that the right horncore lacks its distal quarter. Most bone anterior to the orbits is missing. The left orbit is

complete, while the anterior third of the right orbit is lacking. The basicranium is slightly damaged. More than any other cranium in the Yukon Pleistocene bison collection, this one shows a marked depression of the horncore pedicels, which gives the frontals between the horncores a dome-like appearance. The horncores, although slightly shorter than that of NMC 13506, show a similar lack of curvature. They are slightly backswept so that their distal thirds lie posterior to the occipital plane. A similar backsweep, but not so strong as that common in *Bison crassicornis*, is seen in the holotype of *Bison alaskensis* (Skinner and Kaisen 1947, Plate 24-3). Horncore indices (which I feel are most important in comparing bison crania) of the two Yukon specimens match well.

Discussion

Only seven specimens of *Bison alaskensis* are known. They are from the Dawson and Old Crow areas of the Yukon, and the vicinities of Point Barrow, Fairbanks (Cripple and Engineer creeks), The Ramparts (Walson Creek) and Eschscholtz Bay in Alaska. Therefore, the species was widespread in Eastern Beringia, but evidently it did not last as long or reach such large numbers as *Bison crassicornis*. Little is known about the stratigraphic range of *Bison alaskensis*, but knowledge of

the approximate geological age of a closely allied Eurasian species suggests an early middle to middle Pleistocene age. NMC 13506 was derived from a deep sink in the bed of Gold Run Creek, and bone from it has yielded a radiocarbon date of >39,900 years B.P. (I-5405), suggesting, but not proving that *Bison alaskensis* occupied the Dawson Area before *Bison crassicornis*. All radiocarbon dates on Yukon *Bison crassicornis* lie between approximately 34,000 and 12,000 years B.P. (Table 5).

Although *Bison alaskensis* has not been recorded beyond Eastern Beringia, I wish to point out its affinities with species described from the southern refugium and Eurasia. NMC 13506 and 23349 are very close in indices of horncore curvature, compression, projection and length to the smallest specimens of *Bison latifrons*, which so far, is only known from the southwestern prairies of Canada, the southern and western United States and northern Mexico. If a North American ancestor for *Bison latifrons* is sought, *Bison alaskensis* would be a good choice (Harington and Clulow 1973, p. 735) - it was in the "right" place, at what appears to have been the "right" time, with the appropriate ancestral characteristics.

It is also apparent, when examining the Yukon

Bison alaskensis fossils side by side with a large sample of *Bison crassicornis* crania graded from small to large, that the former species cannot be separated readily from the largest specimens of the latter, except for the tendency of its horncores to be less curved, less backswept, and to be flatter dorsoventrally at the bases. Therefore, it is conceivable that a bison with the cranial characteristics of *Bison alaskensis* could have given rise to both *Bison crassicornis* (by reduction in size in northern regions), and to *Bison latifrons* (by an increase in size in southern regions).

A question arises concerning the origins of *Bison alaskensis*. Has it affinities with Eurasian bison? A specimen of *Bison priscus gigas* that I was able to examine in the Paleontological Institute of the Academy of Sciences of the USSR in Moscow is so like *Bison alaskensis* in size (Table 86) and shape that the two taxa may be synonymous. It is interesting to note that Flerov (1972, p. 85) mentions the similarity of *Bison priscus gigas* and *Bison latifrons*, but disregards the closer morphological and geographical relationships of *Bison priscus gigas* and *Bison alaskensis*. Evidently *Bison priscus gigas* was widespread in Eurasia during the middle Pleistocene (Mindel-Riss (?Yarmouth) interglacial to Riss-Würm (Sangamon) interglacial in Flerov's terminology).

Presumably *Bison alaskensis* was adapted to a cool grassland or parkland habitat.

As a framework for considering the relationships of the four kinds of bison that have been identified from Yukon Pleistocene deposits, I will attempt to summarize some of the major trends in the evolution and dispersal of bison. Much of this information is derived from reasonable discussions of bison phylogeny by Guthrie (1970), Flerov (1972) and Wilson (1974, pp. 140-142). I emphasize that what seems reasonable now is not necessarily correct, and that only more careful biostratigraphic and other geochronological control, coupled with solid statistical studies of bison fossils throughout their time and space ranges, will allow a clearer idea of the evolution of the genus. This, in turn, would provide scientists with increased knowledge of the stratigraphic value of bison fossils. To this end, I propose that an international working group be organized, using standardized procedures for morphological and stratigraphic description.

The earliest known bison greatly resemble *Leptobos* and seem to have diverged from that genus in the late Pliocene of southern Asia. Much of the

evidence is derived from India, where *Probison dehmi* from the upper Pliocene Tatrot beds near Chandigarh is claimed to be the earliest representative of the group (Sahni and Khan 1968, p. 248). The drooping tips of the horncores of this animal seem most peculiar for an ancestral bison, and as there appears to be no contact of the fragmentary left horncore with the cranium (Sahni and Khan 1968, Plate 16-1, 2), perhaps the orientation of the horncore as it is presently restored is subject to doubt. The authors state that *Probison dehmi* is closest to *Bison sivalensis* and that it may be an ancestor of that species.

Bison sivalensis from later (Pinjaur) deposits in northern India, *Bison palaeosinensis* from late Pliocene (Nihowan) beds of China (north of Peking), and *Bison tamanensis* from late Pliocene sediments of the Tamansk Peninsula in the Caucasus are early representatives of this important group of bovids. They were small, slender, *Leptobos*-like animals compared to modern bison, and they may have occupied warm forest environments where forage was soft. In the course of time, the skull broadened, orbits became more tube-like and laterally directed, cheek teeth became longer, and bodies grew more hefty - possibly linked with adaptation to colder

climates and tougher, grassy forage. Flerov (1972, p. 85) suggests that these species be considered as members of the subgenus *Eobison*.

During the early Pleistocene, relatively short-horned bison such as *B. tamanensis*, *B. voigtstedtensis*, *B. langenocornis* and *B. schoetensacki* occupied southern Europe and western Asia. The woodland bison, *Bison schoetensacki*, is known from Waalian interstadial (?mid-Nebraskan) to Würm I (early Wisconsin) time — mainly in Germany. Although this species has been considered as immediately ancestral to the wisent (*Bison bonasus*), recent studies indicate that *Bison schoetensacki* became extinct without issue, and that the modern wisent is a late immigrant from Beringia (Kurtén 1968, pp. 186-187).

During the early to middle Pleistocene, bison with much larger horns (e.g. *B. priscus priscus*, *B. priscus gigas*, *B. alaskensis*) spread widely with the expanding steppe grasslands into northern Eurasia (including northern China) and North America, simultaneously losing ground in southern Asia and ultimately becoming extinct there. Perhaps the "blossoming" of their horns is indicative of a new and well adjusted level of

adaptation to northern grasslands (see V. Geist's "Dispersal Hypothesis"; Geist 1971, p. 287). *Bison priscus*, the steppe bison, was common in Europe, and has been recorded there from deposits of: the Günz II (?late Nebraskan) glacial (e.g. Süssenborn, Hundsheim); the Mindel (?Kansan) glacial (e.g. Mosbach); Holstein (?Yarmouth) interglacial; Riss (Illinoian) glacial; Eem (Sangamon) interglacial; and Würm (Wisconsin) glacial. Toward the end of the last glaciation, before becoming extinct, its range extended from Yorkshire in England to Spain, Italy, Palestine and Siberia.

In Siberia, large bison (*Bison* sp.) are known from the Olyor Suite of Mindel (?Kansan) age, and again occur in the Riss II (late Illinoian) Utkha Beds of that region. During the late Pleistocene (Illinoian to Wisconsin) a bison with the characteristics of *Bison crassicornis* occupied Bolshoi Lyakhov Island in the New Siberian Islands, and the Kolyma Lowland during the early Wisconsin (Iedoma Suite), where it was very common (Sher 1971, p. 209). By this time, smaller-horned, *occidentalis*-like bison appeared. A skull like that of the wood bison, *Bison bison athabasca*, is known from early postglacial sediments on the Bolshaya Chukochya River. Thus, as in North America toward the close of the last glaciation,

bison horncore size (and probably body size) was also reduced in Siberia.

For purposes of the following discussion, it is tentatively assumed that *Bison alaskensis*, and *Bison crassicornis* are subspecies of *Bison priscus*.

Large-horned bison are first recorded from Alaska in deposits that may be of Kansan age (Péwé 1975a, Table 11). Apparently they crossed the Bering Isthmus with many other mammals of Eurasian origin at that time. During the following (Yarmouth) interglacial they penetrated to the plains of southern North America (e.g. *Bison* cf. *latifrons* from Medicine Hat (Stalker and Churcher 1970)). However, bison do not seem to have established themselves on the Great Plains of the United States until early Illinoian time. *Bison latifrons*, the giant bison, evidently was commonest from Illinoian to mid- Wisconsin time in southern North America (Schultz and Lansdown 1972, pp. 398-399). I speculate that a bison like *Bison alaskensis* (? = *Bison priscus gigas*) was the first to enter North America, and that it gave rise to *Bison latifrons* on the southern North American plains toward the close of the Yarmouth interglacial. Again, development of the largest horns known among bison, suggests excellent adaptation to, and exploitation of a fresh, rich environment. The horncores of these giant bison reached a maximum span of 213 cm, compared to

about 66 cm in modern *Bison bison*. A question worth asking is "What were the horncores of female *Bison latifrons* like?". Could some medium-horned fossils ascribed to *Bison chaneyi* and *Bison alleni* actually be females of *Bison latifrons*? Giant bison became particularly abundant and widespread during the Sangamon, ranging from Florida and South Carolina in the east to California and Idaho in the west and Alberta and Saskatchewan in the north. Mid-Wisconsin records are from Texas, California and Alberta (B. Kurtén and E. Anderson, personal communication 1976). *Bison latifrons* survived until late Wisconsin time in Idaho (McDonald and Anderson 1975).

In southern North America, bison began decreasing in size during the late Pleistocene. *Bison alleni* seems to have been derived from *Bison latifrons* toward the end of the Sangamon interglacial. I speculate that *B. alleni* became extinct - giving way to smaller-horned bison from Beringia. These smaller horned bison of the *Bison bison* "*occidentalis - antiquus*" complex spread southward near the close of the Wisconsin glaciation. Perhaps during the hypsithermal period, about 6,000 years ago, most herds of the *Bison bison* "*occidentalis - antiquus*" complex in the north had undergone the transition to wood bison (*Bison bison athabascae*), while southern herds had adapted to the prairie environment, becoming plains bison (*Bison bison bison*).

In Eastern Beringia, *Bison alaskensis* seems to have given way to *Bison crassicornis* by Wisconsin time. As in Siberia, *Bison crassicornis* was very common in the unglaciated parts of the Yukon Territory and Alaska, before it became extinct there about 12,000 years ago. *Bison crassicornis* probably gave rise to the *Bison bison* "occidentalis - antiquus" complex, from which stemmed the modern wood bison, *Bison bison athabasca* in postglacial time. Perhaps the European wisent (*Bison bison bonasus*) and the wood bison (*Bison bison athabasca*) both arose from "occidentalis - antiquus" stock in Beringia - the wisent shifting its range westward and southward, finally adapting to life in the forest; the wood bison spreading eastward and southward along the eastern margins of the Cordillera. Wood bison are known to have lived in the Dawson Area about 1,350 years ago.

Bison crassicornis (large-horned bison)

Fossils of *Bison crassicornis* (called *Superbison crassicornis* by Frick (1937, p. 577) and *Bison (Superbison) crassicornis* by Skinner and Kaisen (1947, p. 187)) are among the most common in the Yukon Pleistocene deposits (Figures 77A-C, 78A-C, 79A-C, Tables 87-91). Obviously herds of these bison were numerous, and ranged widely throughout unglaciated parts of the Yukon, Alaska and Siberia during the late Pleistocene. Specimens described here include only the most complete cranial remains. Also described, and of particular interest, is a collection of well preserved material, including virtually complete crania of male and female *Bison crassicornis*, and postcranial material from a single, high level stratum of late Wisconsin age at Old Crow Locality 11(1). Descriptions of other *Bison crassicornis* cranial and postcranial material from the Yukon are provided by Clark (1927), Williams (1937), and Harington and Clulow (1973).

Referred specimens

Adult male crania - NMC 17688 from Old Crow Locality 11(1) is complete except for the tip of



Figure 77. A. Restoration of large-horned bison
(*Bison crassicornis*) males fighting. Ink
sketch by Bonnie Dalzell.

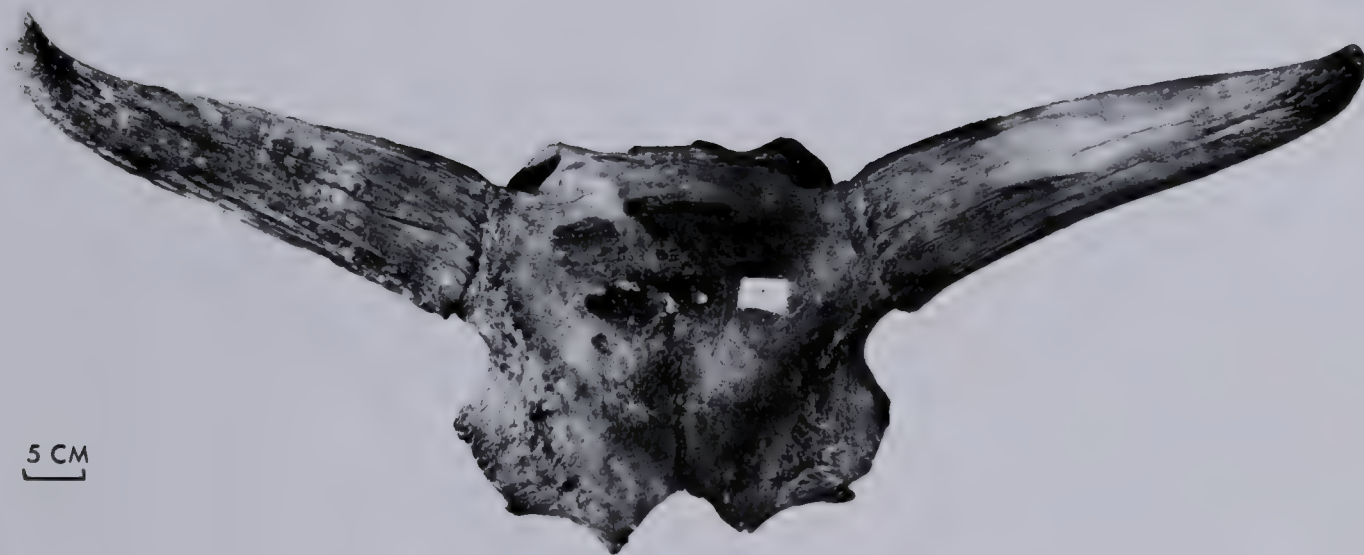
Posterior of cranium with complete horncores
(NMC 7392, Dawson Locality 32) of a male
Pleistocene large-horned bison
(*Bison crassicornis*).

B. Dorsal view (anterior to bottom).

C. Posterior view.



A



B



C



Figure 78. Posterior of cranium with horncores lacking tips (NMC 20634, Old Crow Locality 11(1)) of a male Pleistocene large-horned bison (*Bison crassicornis*).

A. Dorsal view (anterior to top).

B. Posterior view. Sample cut from right horncore was used for x-ray diffraction analysis.

C. Ventral view (anterior to bottom).

Radiocarbon dates on bone from this species at Old Crow Locality 11(1) indicate that this specimen is approximately 12,200 years old.

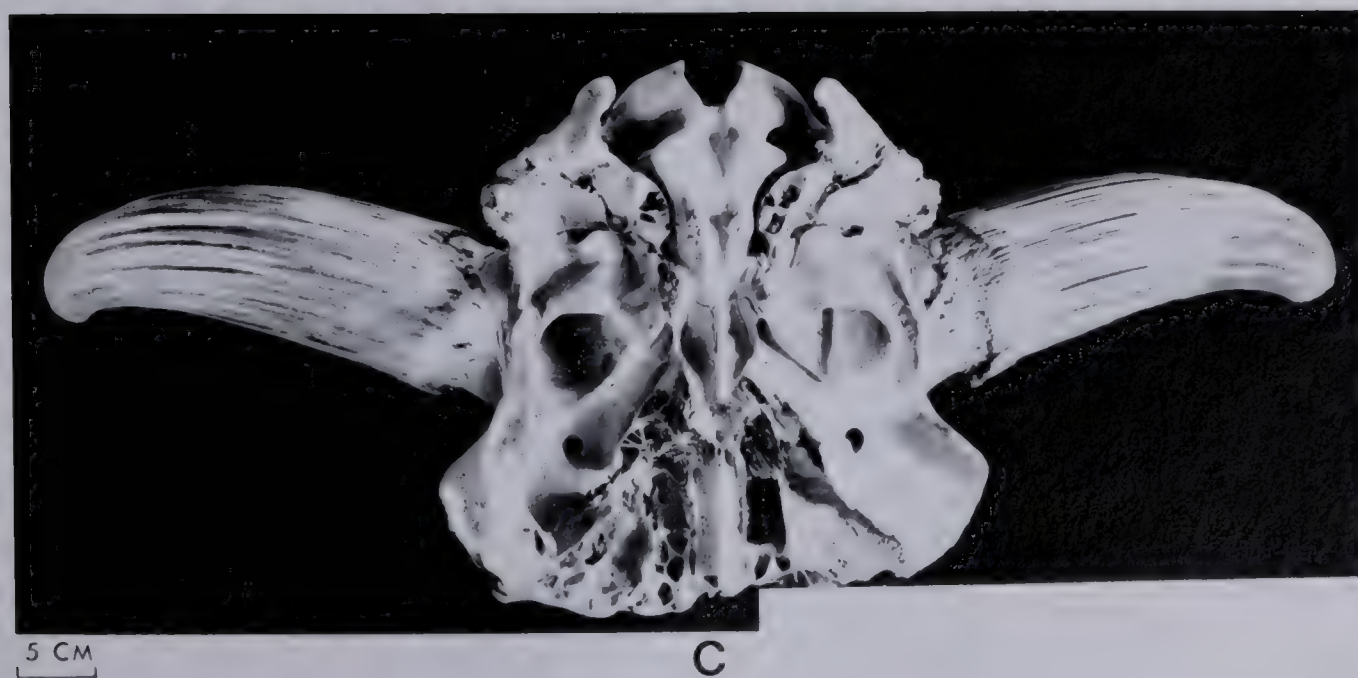
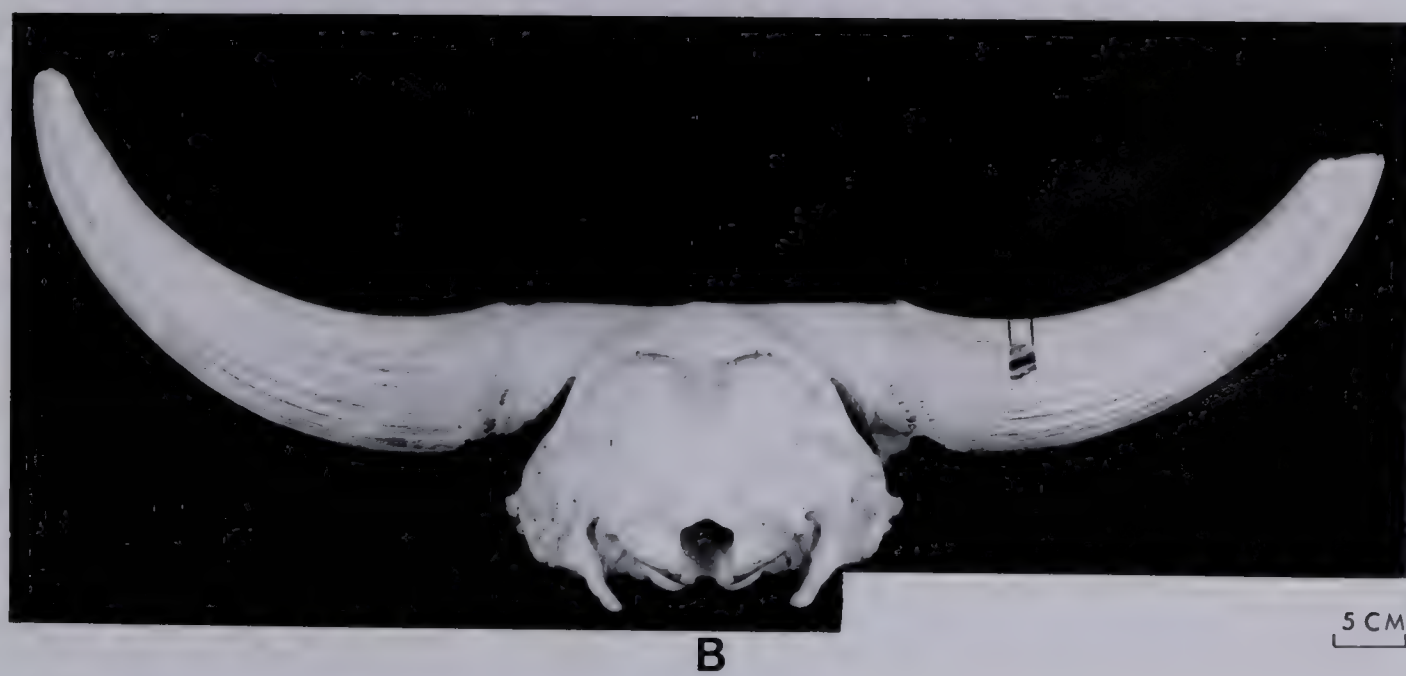
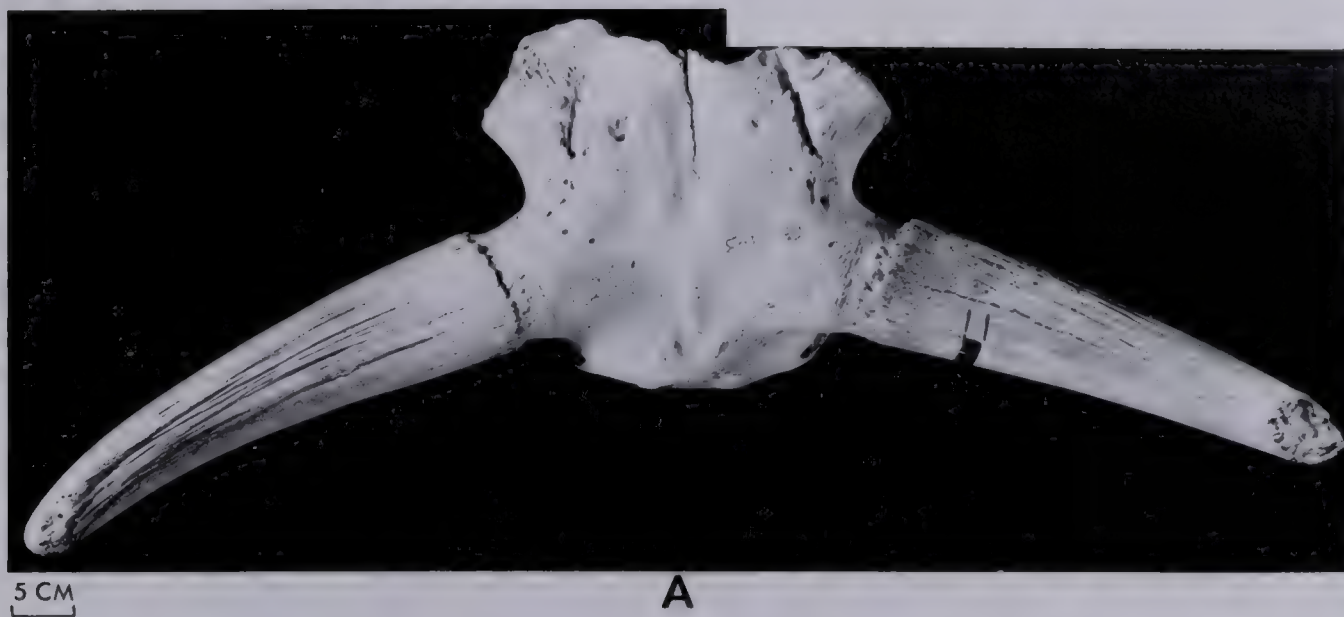




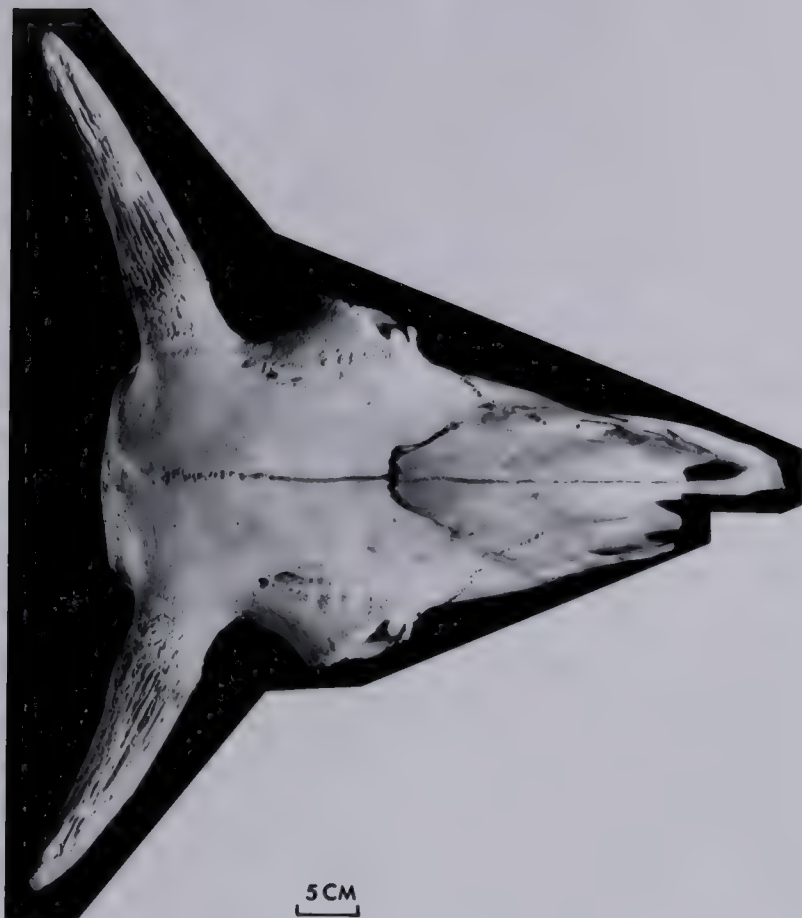
Figure 79. Cranium with horncores and partial horns sheaths (NMC 17687, Old Crow Locality 11(1)) of a female Pleistocene large-horned bison (*Bison crassicornis*).

A. Dorsal view without horns sheaths.

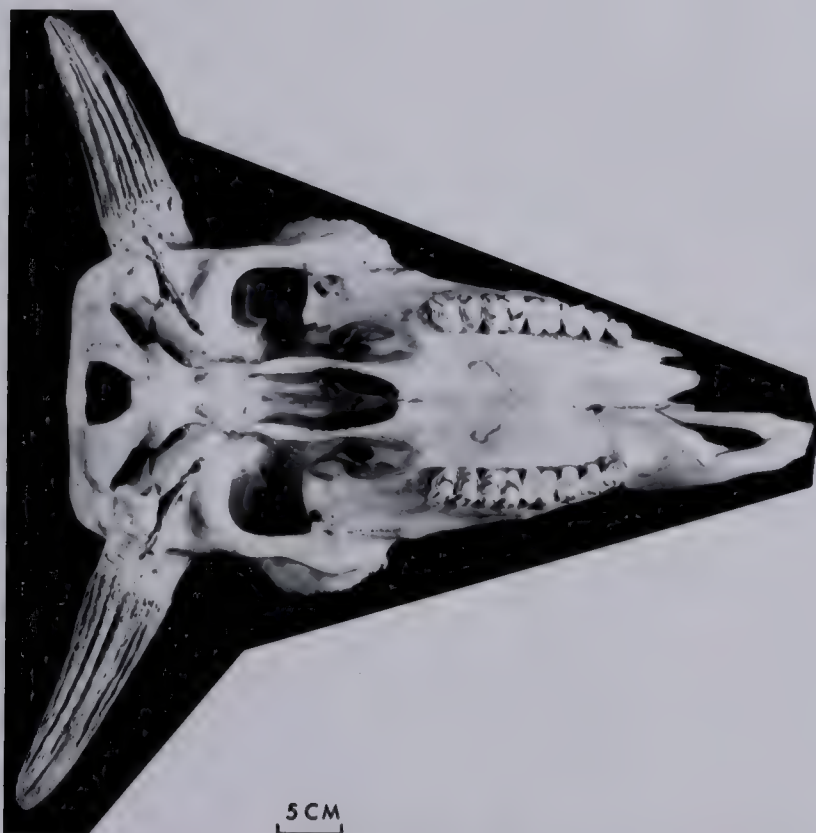
B. Ventral view without horns sheaths.

C. High posterior view with horns sheaths.

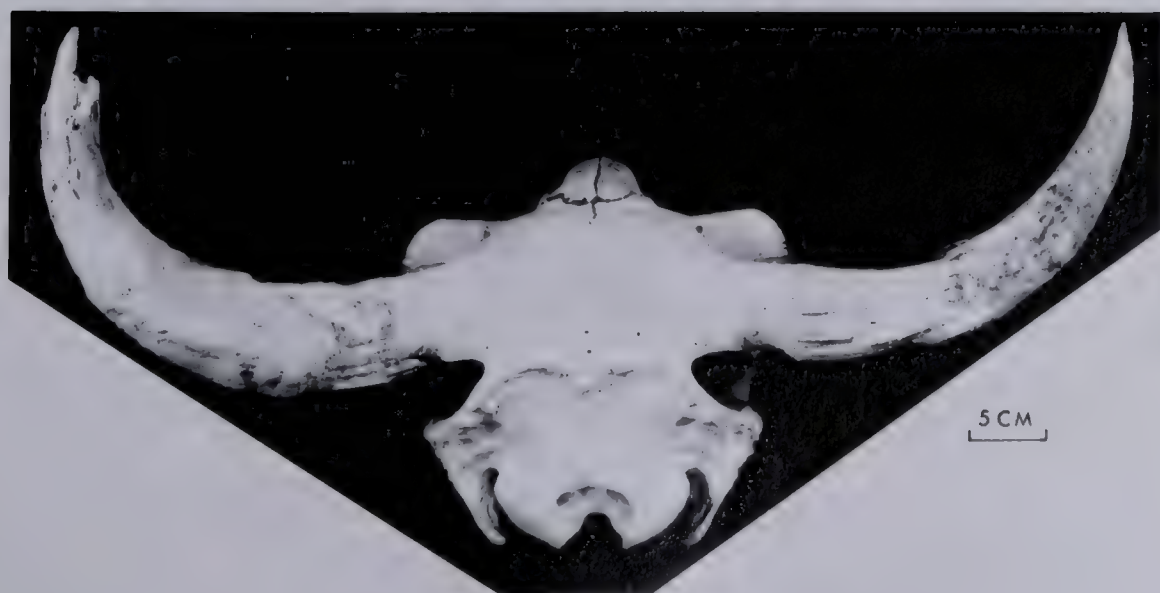
Radiocarbon dates on bone from this species at Old Crow Locality 11(1) indicate that this specimen is approximately 12,200 years old.



A



B



C

Table 87. Measurements of Pleistocene large-horned bison (*Bison crassicornis*) crania from the Yukon Territory.

SPECIMENS	SEX	ESTIMATED AGE	MEASUREMENTS (mm) *																															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30		
<i>Bison crassicornis</i> , Pleistocene, Y.T.																																		
MALES																																		
NMC 7392 Dawson Loc. 39	♂	Adult	946	985	463	520	400	99	120	350	291	-	77	108	151	-	309	365	274	-	-	-	-	-	-	-	-	-	280	130	83	132	150	
NMC 31009 Dawson Loc. unknown	♂	Adult	975	1000	460	520	420	108	125	375	282	150	97	102	149	300	299	356	-	-	-	147	99	-	-	-	-	-	-	-	124	86	123	154
NMC 11675 Dawson Loc. 15	♂	Adult	1080e	1088e	452	480	423	100	112	340	-	-	-	-	-	-	300e	-	-	-	-	-	-	-	-	-	-	-	-	-	114	89	133	151e
NMC 11646 Dawson Loc. 32	♂	Adult	-	-	440	503	396	100	122	349	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	127	82	126	-	
NMC 11674 Dawson Loc. 15	♂	Adult	-	-	439	510	390	101	118	350	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	131	86	125	-
NMC 8145 Dawson Loc. 3	♂	Adult	970	988	435	490	377	93	102	310	262	135	73	104	152	338	292	-	-	-	-	-	-	-	-	-	-	-	-	-	130	91	140	149
NMC 7393 Dominion Ck. (Dawson Area)	♂	Adult	996	1016	420	495	362	95	105	320	-	-	-	-	-	373	301	352	276	-	-	-	-	-	-	-	-	-	-	-	137	91	131	140
NMC 10458 Dawson Loc. 12	♂	Adult	-	-	419	476	370	106	119	355	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	129	89	118	-
NMC 17330 Dawson Loc. 6	♂	Adult	1070	1074	415	460	375	101	121	358	-	154	85	113	157	346	-	-	-	-	-	-	-	-	-	-	-	-	-	-	123	84	116	-
NMC 8144 Dawson Loc. 3	♂	Adult	747	823	413	475	340	91	108	312	-	132	71	105	145	293	275	-	-	-	-	-	-	-	-	-	-	-	-	-	140	84	132	150
NMC 17602 Dawson Loc. 28	♂	Adult	-	-	410	474	353	101	112	341	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	134	90	120	-
NMC 20634 Old Crow Loc. 11(1)***	♂	Adult	960e	1000e	410	460	380	96	107	322	271	133	91	114	155	302	272	340	-	-	-	-	-	-	-	-	-	-	-	-	121	90	127	151
NMC-17683 Old Crow Loc. 11(1)***	♂	Adult	880	890e	400	465	345	91	95	290	265	130	69	105	155	305	276	333	-	182	129	153	92	158	532	566	490	267	135	96	138	145	-	
NMC 26192 Old Crow Loc. 11(1)***	♀	Adult	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	192	-	147	90	-	-	-	-	-	-	-	-	-	-	
NMC 13507 Dawson Loc. 32	♂	Adult	-	-	400	445	370	96	106	321	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	120	91	125	-	
NMC 24202 Old Crow Loc. 11(1)***	♂	Adult	940e	980e	390	440	350	88	94	293	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	126	94	133	-
NMC 24200 Old Crow Loc. 11A	♂	Adult	-	-	385	445	361	101	110	330	-	-	84	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	123	92	117	-
NMC 11683 Brewer Loc. 1	♂	Adult	-	-	380e	435e	335e	90	99	298	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	130e	91	128e	-
NMC 7700 Dawson Loc. 9	♂	Adult	990	995	380	419	352	91	98	295	-	149	74	104	150	333	288	-	-	-	-	-	-	-	-	-	-	-	-	-	119	93	129	132
NMC 11782 Dawson Loc. 28	♂	Adult	-	-	370	447	322	98	116	332	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	139	85	111	-
NMC 11352 Dawson Loc. 2	♂	Adult	-	-	365	410	336	93	111	324	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	122	84	113	-
NMC 8874 Indian R. (Dawson Area)	♂	Adult	960e	990e	360e	400e	330e	95	103	307	262	127	69	101	140	344	276	-	-	-	-	-	-	-	-	-	-	-	-	-	121e	92e	117e	130e
NMC 17689 Porcupine Loc. 40	♂	Adult	-	-	358	414	319	87	100	297	-	138	75	105	154	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	130	87	121	-
NMC 11351 Dawson Loc. 2	♂	Adult	-	-	354	373	332	81	108	300	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	112	75	118	-
NMC 9885 Dawson Area	♂	Adult	900	914	353	405	327	91	109	313	-	142	70	100	142	320	292	-	-	-	-	-	-	-	-	-	-	-	-	-	124	84	113	121
NMC 13503 Dawson Loc. 32	♂	Adult	-	-	350	430	300	89	101	302	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	143	88	116	-
NMC 11782 Dawson Loc. 28	♂	Adult	-	-	350e	400e	310e	96	117	334	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	129e	82	105	-
NMC 13559 Dawson Loc. 32	♂	Adult	-	-	347	411	300	95	116	337	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	137	82	103	-
NMC 9923 Dawson Loc. 12	♂	Adult	-	-	338	365	320	85	109	304	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	114	78	111	-
NMC 8146 Dawson Loc. 5	♂	Adult	770	780	335e	375e	295e	89	106	309	270	133	76	93	138	182	279	-	-	-	-	-	-	-	-	-	-	-	-	-	127e	84	108e	120e
FEMALES																																		
NMC 17687 Old Crow Loc. 11(1)***	♀	Adult	622	625	205	235	203	66	63	207	229	134	74	91	131	262a	222	285	214	168	119	148	91	151	501	540	560	235	116	105	99	92	-	
NMC 11783 Dawson Loc. 28	♀	Adult	-	-	190	215	184	59	60	193	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	117	98	98	-
FEMALES OR IMMATURE MALES?																																		
NMC 13705 Old Crow Loc. 11A (probably derived from Loc. 11(1)***)	♀	?Immature	720e	740e	295	343	280	77	79	248	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	123	98	119	-	
NMC 17331 Dawson Loc. 7	♀	?Immature	710e	715e	294	223	270	70	113	226	-	123	65	96	139	248	240	-	-	-	-	-	-	-	-	-	-	-	-	-	120	96	130	123
NMC 11360 Dawson Loc. 2****	-	-	-	-	278	310	260	57	65	187	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	119	88	149	-
NMC 11687 Stewart Loc. 3	-	-	-	-	258	303	235	61	58	189	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	129	105	137	-
NMC 25193 Dawson Loc. 16	-	-	-	-	248	283	234	61	68	209	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	121	90	119	-
NMC 17601 Dawson Loc. 28	-	-	-	-	230e	270e	220e	62	64	202	-	-	-	-	-	291	239	303	-	-	-	-	-	-	-	-	-	-	-	-	123e	97	114e	96
NMC 25169 Dawson Loc. 33	-	-	-	-	210	253	200	56	54	177	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	127	104	119	-
JUVENILE																																		
NMC 25180 Dawson Loc. 16	-	Juvenile	-	-	102e	104e	102e	37e	44e	132e	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	102e	84e	77e	-

* See measurements with Table 86.

** See Table 36 for comparative statistical measurements on adult male *Bison crassicornis* crania from the Pleistocene of Alaska and the Yukon Territory.

*** Specimens derived from a deposit of late Wisconsin age radiocarbon dated at approximately 12,000 years B.P.

**** This horncore is twisted approximately 90° forward from its normal position. It is measured as if it were in the usual orientation.

Table 88. Measurements of Pleistocene large-horned (*Bison crassicornis*) maxillae and mandibles with teeth from Old Crow Locality 11(1), Yukon Territory.

SPECIMENS	SEX	AGE CLASS	MEASUREMENTS (mm) *																								
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	
<i>Bison crassicornis.</i> Pleistocene, Y.T.																											
<u>MAXILLAE</u>																											
NMC 17688	♂	S-3	16.6	15.4	21.9	20.5	19.5	18.4 ⁺	19.5	21.4	20.0 ⁺	27.7	24.5	21.9 ⁺	33.3	23.9	21.8 ⁺	32.9	24.0	23.3 ⁺	-	-	-	-	-	-	-
NMC 17687	♀ ⁺	S-3	18.2	14.3	6.9	19.6	20.9	8.0	17.1	23.1	8.8	24.5	25.7	10.1	29.7	27.7	21.0	33.8	27.0	17.3 ⁺	-	-	-	-	-	-	-
NMC 26192	-	S-4	-	-	-	-	-	-	-	-	-	24.1e	26.1	10.6	30.3	29.2	16.6	32.2	28.0	18.6 ⁺	-	-	-	-	-	-	-
<u>MANDIBLES</u>																											
NMC 23019	-	S-4	-	-	-	17.6	11.7	9.3	21.2	13.7	8.6	27.0	19.4	8.7	32.8	21.5	9.3	46.3	20.0	22.1 ⁺	456.0a	190.7	62.1	34.6	156.0a	164.2	
NMC 26107b	} same individual	S-3	12.4	9.8	13.3	18.9	11.9	11.5	22.5	15.4	12.2	25.7	18.9	11.9	31.2	21.9	14.0	46.3	20.2	15.5	457.0a	195.2	52.5	29.9	153.0a	160.1	
NMC 26107a		S-3	12.6	9.9	11.6	19.0	12.3	9.6	22.2	15.0	12.0	25.0	18.9	12.2	30.5	21.8	16.0	46.7	19.9	19.4	457.0	195.6	53.3	24.3	153.0a	162.7	
NMC 26136		S-4	-	-	-	-	-	-	-	-	-	-	-	-	-	30.8	19.9	14.9	-	-	-	440.0	190.9	38.0**	34.6	161.0a	153.5

* 1. Maximum length P2. 2. Maximum width P2. 3. Maximum height P2 (from cingulum to crown on lingual side. Heights with a plus (+) sign indicate height of tooth crown above alveolar margin when cingulum is not exposed). 4. Maximum length P3. 5. Maximum width P3. 6. Maximum height P3. 7. Maximum length P4. 8. Maximum width P4. 9. Maximum height P4. 10. Maximum length M1. 11. Maximum width M1. 12. Maximum height M1. 13. Maximum length M2. 14. Maximum width M2. 15. Maximum height M2. 16. Maximum length M3. 17. Maximum width M3. 18. Maximum height M3. 19. Mandible length posterior of angle to anterior tip. 20. Distance from posteriormost surface of condyle to posterior alveolar margin of M₃. 21. Mandible depth below centre of M₁. 22. Mandible width below centre of M₁. 23. Length from anterior of P₂ alveolus to anterior tip of mandible. 24. P₂-M₃ alveolar length.

** Unusual shallowness results from pathological condition.

Table 89. Measurements of Pleistocene large-horned bison (*Bison crassicornis*) vertebrae from Old Crow Locality 11(1), Yukon Territory.

Specimens	Measurements (mm)*				
	1	2	3	4	5
<i>Bison crassicornis</i> . Pleistocene, Y.T.					
<u>Atlas</u>					
NMC 26114	110.3	227.0e	135.0	50.1	39.0
NMC 23338	103.7	198.9	135.5	49.8	43.2
<u>Axis</u>					
NMC 17170	189.0	150.5	135.8	132.4	102.0
NMC 26115	176.0	142.0	131.8	116.0e	88.1
<u>Fifth Cervical</u>					
NMC 17196	189.2	186.2	-	84.8	77.0
<u>?First Thoracic</u>					
NMC 26125	619.0	131.0	-	77.0	548.0
<u>?Third Thoracic</u>					
NMC 26126	619.0	125.9	-	76.7	551.0
<u>?Fifth Thoracic</u>					
NMC 26171	496.0	119.6	-	75.9	438.0
<u>Sacrum</u>					
NMC 17159	185.4	293.8	-	293.5	99.1
NMC 26178	180.2	244.4	-	237.0 [†]	77.2

* 1 - Maximum height.

2 - Maximum width.

3 - Maximum width across occipital condylar facets (atlas) or anterior articular processes (axis).

4 - Straight-line, mid-ventral length below the neural canal.

5 - Height of dorsal tubercle (atlas) or neural spine from anterior dorsal surface of neural canal to top of tubercle or neural spine.

Table 90. Measurements of Pleistocene large-horned bison (*Bison crassicornis*) scapulae from Old Crow Locality 11(1), Yukon Territory.

Specimens	Measurements (mm)*					
	1	2	3	4	5	6
<i>Bison crassicornis</i> .Pleistocene, Y.T.						
NMC 22854	82.9	67.5	105.3	90.7	35.4	558.0
NMC 20444	84.0	70.2	105.5	93.0	40.5	536.0†
NMC 17171	83.1	71.7	104.8	87.9	36.8	478.0†
NMC 22886	76.1	66.3	92.6	79.8	33.9	469.0†
NMC 26166	80.1	64.0	98.2	71.8	31.1	446.0

- * 1 - Maximum length of glenoid fossa.
- 2 - Maximum width of glenoid fossa.
- 3 - Maximum length of scapula taken at a point between glenoid fossa and neck.
- 4 - Minimum length at neck.
- 5 - Minimum width at neck.
- 6 - Maximum height of scapula (anterior margin of glenoid cavity to vertebral border).

Table 91. Measurements of Pleistocene large-horned bison (*Bison crassicornis*) limb bones from Old Crow Locality 11(1), Yukon Territory.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Bison crassicornis</i> .							
Pleistocene, Y.T.							
<u>Humeri</u>							
NMC 29273	424.0	130.8	127.3	55.7	70.0	105.5	106.6
NMC 29274	433.0	-	-	58.0	63.5	108.5	103.6
NMC 23020	361.0	114.0	110.2	48.1	57.9	92.3	95.0
NMC 26127	357.0	110.2	113.8	46.1	56.4	94.3	94.7
<u>Radii</u>							
NMC 17160	389.0(505.0)**	117.4	59.8	60.8	40.6	108.5	67.3
NMC 29276	386.0(504.0)**	115.0	63.4	64.7	42.1	106.5	66.7a
NMC 17194	385.0	112.8	58.3	57.2	39.0	102.5	67.0
<u>Metacarpals</u>							
NMC 29272	230.0	84.8	51.1	55.2	34.5	88.4	45.0
NMC 22851	228.2	84.7	49.3	50.1	36.4	84.7	45.0
NMC 20439	218.7	71.2	44.2	42.1	30.7	75.0	40.5
<u>Femora</u>							
NMC 26108	502.0	164.5	75.2	48.8	55.5	128.6	167.0
NMC 22853	427.0	131.6	61.1	41.1	43.3	104.1	143.5
<u>Tibiae</u>							
NMC 26168	436.0	134.1	120.7	54.3	45.8	82.6	62.1
NMC 17178	431.0	122.8	115.9	49.5	41.5	78.7	58.0
NMC 26167	422.0	122.2	113.7	50.0	46.1	75.8	58.4
NMC 26177	414.0	125.0	115.1	50.0	45.2	76.6	60.0
<u>Metatarsal</u>							
NMC 20437 (immature)	228.6 ⁺	50.1	49.6	29.9	30.6	-	-
<u>First Phalanges</u>							
NMC 26182	82.4	42.1	46.7	34.8	24.3	38.0	30.1
NMC 17188	78.2	43.4	44.0	38.8	26.4	41.1	31.7
NMC 26113	75.4	39.8	43.4	36.1	28.2	40.8	31.8

* 1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Midshaft (minimum shaft in humeri) width.

5 - Midshaft (minimum shaft in humeri) depth.

6 - Distal width.

7 - Distal depth.

** Total length of entire radio-ulna.

the left horncore, RP², and damage to the anterior part of the left orbit. According to Skinner and Kaisen's (1947, p. 145) method of age classification for plains bison (*Bison bison bison*), the individual represented by this specimen was at the beginning of full maturity (S-3). The fossil is generally fresh in appearance, being tan to rust colored on the surface. It is of late Wisconsin age. NMC 20634 from Old Crow Locality 11(1) is a cranial fragment with horncores. It lacks bone anterior to the orbits. Although the tip of the right horncore is missing, the spread from tip to tip of the horncore is much greater than that of NMC 17688. A small slice of bone was removed from the right horncore for x-ray diffraction analysis, in order to ascertain the types and relative concentrations of various elements in the bone. NMC 24204 from Old Crow Locality 11(1) is a left horncore with most of the left frontal attached. The upper part of the orbit is preserved. The bone varies in color between tan and rust. It is of late Wisconsin age.

NMC 31000 from an unknown locality in the Dawson Area is a cranial fragment with horncores, the right facial region including the orbit, chipped RM²-RM³ and alveoli for RP²-RM¹, and adjacent palatal bone. A

virtually complete left nasal (225 mm long x 60 mm wide) may belong with NMC 31000, but there are no contacts with the rest of the cranium, so this association must remain conjectural. NMC 8144 from Dawson Locality 3 is a posterior cranial fragment with horncores and the distal halves of both hornsheaths. Bone anterior to the orbits is lacking and the occipital and basicranial regions are damaged. The inward, backward curving tips of the hornsheaths, when in place, are 500 mm apart, and the greatest spread on the outside curve of the hornsheaths is 847 mm. NMC 8874 from Indian River near Dawson is a posterior cranial fragment with horncores and hornsheaths. The anterior margin of the right hornsheath is damaged. Most of the left orbit is lacking, whereas only the dorsal portion of the right orbit is preserved. The tips of the hornsheaths, when in place, are 790 mm apart, and the greatest spread on their outside curve is 1,062 mm.

NMC 7393 from Dominion Creek in the Dawson Area, was collected 30 feet (9.1 m) below the surface. It consists of the posterior dorsal portion of a cranium with horncores and complete hornsheaths. Most of the bone anterior to the nasofrontal suture is lacking. The left orbit is complete but only the dorsal half of the right one is preserved. The tips of the hornsheaths, when in place, are 795 mm apart, and the greatest spread

on their outside curve is 1,070 mm. They are approximately 460 mm long on the inside curve from burr to tip. NMC 8145 from Dawson Locality 3 is a posterior cranial fragment with horncores and nearly complete hornsheaths. Bone anterior to the orbits is lacking and the basicranium is badly damaged. The left orbit is complete, but most of the right orbit is missing. The tips of the hornsheaths are 747 mm apart, and the greatest spread on their outside curve is 1,037 mm. They are approximately 530 mm long on the inside curve.

NMC 17330 from Dawson Locality 6 is a posterior cranial fragment with horncores. Bone anterior to the orbits is lacking, and part of the right upper section of the occipital region is damaged. The frontal suture is fused, indicating that the specimen represents an old male. NMC 7700 from Dawson Locality 9 is a posterior cranial fragment with both horncores and the distal half of the left hornsheath. Bone anterior to the orbits is lacking, and little of the orbits remains. Occipital and basicranial regions are slightly damaged. NMC 7392 from Dawson Locality 32 is a posterior cranial fragment with complete horncores and orbits. The right occipital condyle is missing. The fossil was collected by

R.G. McConnell in 1900. It came from muck 15 feet (4.6 m) below the surface on claim 17 of Gold Run Creek. Whiteaves (1903, p. 240) remarked that this specimen (designated as Museum of the Geological Survey No. 1 for convenience at that time) is larger and much longer-horned than skulls of Recent wood or plains bison, and stated that it is "apparently referable to the form which Mr. Rhoads describes and figures as the 'Great Alaskan Bison,' *Bison alaskensis*..." However, he noted that Lucas (1899) had placed *B. alaskensis* among the synonyms of *B. crassicornis* Richardson. Skinner and Kaisen (1947, p. 196), calling the specimen "Mus. Geol. and Surv. Canada 1," correctly referred it to *B. crassicornis*. NMC 9885 from the Dawson Area (exact locality unspecified) is a posterior cranial fragment with horncores. Bone anterior to the severely damaged orbits is lacking. The basicranial region is damaged.

NMC 8146 from the Dawson Area (exact locality unspecified) is a posterior cranial fragment with horncores. Bone anterior to the constriction between the horncores and orbits is lacking, the basicranium is damaged and the central part of the skull is partly split lengthwise. The fossil has relatively short horncores for an adult male - which it seems to represent

according to the well defined horncore burrs. Yet other characteristics, such as the marked backsweep of the deeply-grooved, sharp-tipped horncores, and the indices of horn-core curvature, compression, proportion and length, which are within the range of *B. crassicornis* (Skinner and Kaisen 1947, Table 16), indicate it is a small *Bison crassicornis* cranium.

Referred left horncores - NMC 13507 from Dawson Locality 32 is attached to the left half of a cranial fragment extending from the posterior of the left orbit to the occipital region. The bone is stained rusty brown. NMC 13508 from Dawson Locality 32 is attached to the left half of a dorsal cranial fragment extending from the orbit to the posterior margin of the frontal. It is stained dark reddish brown. NMC 11782 from Dawson Locality 28 is similar to NMC 13508 except that a heavily eroded hornsheath is attached. NMC 24200 from Old Crow Locality 11A is attached to the left half of the dorsal part of the braincase, including part of the left orbit. Bone on the inner surface of the orbit and on the left frontal is deeply pitted. Small parts of the right occipital region, including the right occipital condyle, are present. The specimen is stained dark reddish brown. It appears to be of late Wisconsin age.

NMC 17602 from Dawson Locality 28 is attached to large parts of both left and right frontals. Only small fragments of the orbits are preserved. The specimen is iron-stained and weathered. NMC 11646 from Dawson Locality 32 is attached to a left frontal. It is dark rust in color. Erosion on the upper surface of the burr partly accounts for its relatively high degree of compression.

Referred right horncores - NMC 11674 from Dawson Locality 15 is attached to the frontal, and includes part of the right orbit. NMC 10458 from Dawson Locality 12 is similar to NMC 11674. It is stained dark brown. NMC 17689 from Porcupine Locality 40 is attached to the right frontal and most of the occipital and basicranial regions. It is reddish brown. NMC 11683 from Brewer Locality 1 is attached to the posterior half of a right frontal. The tip of the horncore is slightly damaged. NMC 13559 from Dawson Locality 32 is attached to the right and part of the left frontals. It is reddish brown with black (manganese?) patches. NMC 11782 from Dawson Locality 28 is attached to the lateral half of the right frontal, including part of the orbit. Its heavily eroded and weathered horns sheath has the inward and backward twist at the tip that is

characteristic of *Bison crassicornis*. The tip of the horncore is probably lodged in the anterior of the hornsheath. An abnormal (pathological?) depression is seen on the ventral surface of the horncore, between 50 mm and 110 mm from the burr. The specimen is stained rusty brown. NMC 9923 from Dawson Locality 12 is attached to a small fragment of the right frontal. It is iron-stained.

Adult female crania referred - NMC 17687 from Old Crow Locality 11(1) was derived from the same late Wisconsin stratum as the well preserved adult male cranium NMC 17688. This cranium is complete except that the right premaxilla and the medial halves of the hornsheaths are lacking. According to Skinner and Kaisen's (1947, p. 145) method of age classification for plains bison, the individual represented by the cranium was in full maturity (S-3). The loops of the lingual styles of M^1 s have disappeared into the enamel borders of the roots, and the lingual styles of M^3 s are moderately worn. Burrs are poorly developed. The horncores are shorter and more slender than those of males of the same age class from the same radiocarbon-controlled late Wisconsin deposit. When in place, the tips of the hornsheaths are 655 mm apart. They do not rise so high or curve so far inward and backward at the tips as do

male adult *Bison crassicornis* horns. The greatest length across the outside curve of the horns sheaths is 705 mm. The length of a complete horns sheath along the upper curve is estimated to be 370 mm - about 45% greater than the same measurement of the horncores, and approximately 70% the length of an adult male *Bison crassicornis* horns sheath (NMC 8145). The surface of the bone of NMC 17687 is tan to reddish brown and has a very fresh appearance. NMC 11783 from Dawson Locality 28 is a right horncore with a small posterior fragment of the right frontal. A very deep groove exists on the ventral surface of the horncore. The fossil matches well the horncores of the adult female NMC 17682 and is referred to a female of *B. crassicornis*. The indices of horncore curvature, compression and proportion between NMC 11783 and 17682 are very close (Table 87). The specimen is stained yellowish tan.

Immature male or adult female crania referred - NMC 13705 was recovered from the surface at the upstream end of a gravel bar (Old Crow Locality 11A). The relatively fresh appearance of the bone matches that of other *Bison crassicornis* material from Old Crow Locality 11(1), and most likely it was derived from that site, which is a short distance upstream on the same side of the river.

The fossil consists of a right horncore and a right frontal fragment showing part of the frontal suture and extending forward to the orbit. The frontal suture appears to have been open when the animal died (this cannot be established with certainty), cranial bone is relatively thin, and while the horncore is smaller than any I attribute to adult male *Bison crassicornis*, it is more robust than any specimens that I think are assignable to adult female *B. crassicornis* (particularly in length, degree of burr development, and circumference of the horncore near the base). Therefore, I tentatively consider that the fossil represents an immature male of the large-horned bison. NMC 17331 from Dawson Locality 7 is a posterior cranial fragment with horncores and heavily eroded basicranial and occipital regions. The occipital condyles are worn. Sutures are open except for a small area near the juncture of the frontal and frontoparietal sutures. The length of the horncores and the relatively high indices of proportion and length indicate that the fossil represents an immature male rather than a female, and I tentatively refer it to an immature male of *Bison crassicornis*. The bone is light buff with occasional patches of iron staining.

I am not sure of the sex or age of the following

specimens, but the horncore size and shape suggest that they are attributable to either immature males or mature females of *Bison crassicornis*. NMC 17601 from Dawson Locality 28 is the dorsal surface of a posterior cranial fragment with small horncores, the tips of which are missing. Sutures present are in the same condition of fusion as those of NMC 17331 but the horncores are rather smaller. NMC 25193 from Dawson Locality 16 is a left horncore with a small portion of the left frontal. It is stained light brown. NMC 25169 from Dawson Locality 33 is a left horncore with part of the left frontal, and most of the hornsheath. NMC 11687 from Stewart Locality 3 is a left horncore with part of the left frontal, including a lateral fragment of the orbit, and a small part of the parietal. The specimen is deep reddish brown. NMC 11360 from Dawson Locality 2 is an aberrant right horncore. It is twisted forward approximately 90° from its usual orientation, matching well the condition in a partial, referred female *Bison crassicornis* cranium from Pleistocene deposits of Alaska. In that specimen the left horncore is normal, whereas the right one is twisted forward (Skinner and Kaisen 1947, Plate 23-4, 4a). I speculate that there is genetic control of the orientation of the horncore, which was not regularly expressed in these cases. The evidence

also suggests that genetic control for one horncore can be autonomous from that for the other horncore. On the other hand it could be an embryogenetic abnormality. NMC 11360 is stained dark brown and may be older than most Pleistocene mammal specimens from the Dawson Area.

I tentatively refer NMC 25180 from Dawson Locality 16, a small, slightly damaged left horncore with part of the left frontal, to a juvenile of *Bison crassicornis*. The shortness of the horncore, which is best described as a "spike", indicates that the fossil represents a calf only a few months old. It belongs in Skinner and Kaisen's (1947, p. 143, Plate 8-2) "immature (I-S)" category, and suggests that large-horned bison calved in the Dawson Area during the late Pleistocene. The fossil is stained dark reddish brown.

Following are descriptions of the best preserved mandibles and postcranial elements of bison from Old Crow Locality 11(1). The specimens are of particular interest because they can be identified definitely as belonging to *Bison crassicornis*, and almost certainly they are members of a single population - perhaps a single herd. Further, they are the last known representatives of *Bison crassicornis* in the Yukon Territory, having been radiocarbon dated at approximately 12,000 years B.P.

Unless otherwise specified, the bones are tan in color and fresh in appearance. Cranial material from this site has been described above with the other large-horned bison crania.

Before describing the mandibles and postcranial material, it is advisable to provide some geochronological background. Radiocarbon analyses of bison bone from the site yielded dates of $11,910 \pm 180$ years B.P. (I-7765) and $12,460 \pm 220$ years B.P. (I-3574). A horncore from a *Bison crassicornis* cranium located near the surface of the first gravel bar (Locality 11A) downstream from Locality 11(1), and presumably washed down from that site during the spring flood, gave a radiocarbon date of $12,275 \pm 180$ years B.P. (I-7764). This concentration of fossils may have resulted from a herd of bison breaking through lake ice and dying, their bones eventually being transported a short distance downslope to the present locality. It is worth noting that in Wood Buffalo Park, many bison are known to have drowned by breaking through thin or rotting ice in early winter or late spring (Fuller 1962, p. 38), which may lend some credence to my suggestion.

Mandibles - NMC 23019 is a left mandible with LP_3 - LM_1 and the alveolus for LP_2 . It is complete except for LP_2 and slight damage to the posterior margin of the angle, the tip of the coronoid process, and the anterior tip of the mandible. Enamel patterns are virtually obliterated on the occlusal surfaces of LP_3 - LM_1 . Using age class criteria

established by Skinner and Kaisen (1947, p. 146) for plains bison mandibles (which I think are roughly applicable in this case), NMC 23019 represents an animal in early part of the "old age (S-4)" category. NMC 26107b is a left mandible with LP_2-LM_3 . It is complete except for slight damage to its anterior tip. The specimen articulates with NMC 26107a, a complete right mandible with RP_2-RM_3 , forming an entire lower jaw. It belongs in Skinner and Kaisen's "full maturity (S-3)" category. NMC 26136 is a right mandible with RM_2 , the posterior root for RM_1 and alveoli for the remaining cheek teeth. The most remarkable feature of this specimen is the severe erosion of the mandibular bone in the RP_4-RM_1 region. Consequently, the depth of the mandible below the position of RM_1 is about half the depth below RM_2 . This condition appears to be pathological, perhaps resulting from periodontal erosion following the loss of RP_4 and RM_1 . As if in compensation for the shallowness of the mandible in this region, evidently the jaw thickened laterally, where a surficial vascular pattern indicates callus may have developed. Miller (1974, Figure 5-6) illustrates cases of dental malocclusion in 8-year-old caribou resulting from loss of anterior cheek teeth and tooth decay, which are reminiscent of the condition in NMC 26136. Disregarding possible pathological effects, the heavy wear on RM_2 suggests that the bison represented by the fossil was in the "old age (S-4)" category. The comparatively short RP_2-RM_3 alveolar length is also indicative of an old individual.

Vertebrae - Two atlas vertebrae are in the collection. NMC 26114 is damaged on the right lateral margin. Rootlet impressions cover its surface, suggesting decay in a grass-land environment. NMC 23338 is complete, but smaller than NMC 26114. Two axis vertebrae include: NMC 26115, which is complete except for the posterior epiphyseal plate of the centrum; and NMC 17170, which is complete and appears to represent a large animal. Other vertebrae in the collection include: a complete fifth cervical (NMC 17196); a ?first thoracic (NMC 26125), which may lack the tip of the neural spine; a complete ?third thoracic (NMC 25126); a complete ?fifth thoracic (NMC 26171). These fossil vertebrae were compared to their counterparts in a modern *Bison bison* skeleton (NMC 5552) from Alberta. All of the fossils were markedly larger. Two nearly complete sacral elements are present. NMC 17159 is the larger. The anterior margin of the first of the fused neural spines is slightly damaged. NMC 26178 seems to be from an immature or female according to its small size, and the relative thinness of the bone. The last (fifth sacral) vertebra has been broken off.

Scapulae - NMC 22854 is a complete right scapula (except, of course, for the scapular cartilage). NMC 26166 is a right scapula of a smaller individual. It lacks the acromion and bone near the central part of the vertebral border. The anterior angle is slightly eroded. NMC 20444 is a left scapula of comparable size to NMC 22854. It is complete except for part of the vertebral border. NMC 17171,

a left scapula, is complete except for the tip of the acromion and the margins of the anterior angle and vertebral border. Unlike the other specimens, the left scapula NMC 22886 shows signs of weathering and surface cracking. It is damaged near the anterior angle, and along the vertebral border extending into the central part of the infraspinous fossa.

Humeri - Of four left humeri from Old Crow Locality 11(1), two are small (female?) and two are large (male?). NMC 29273, one of the larger specimens, is complete. NMC 29274 is of similar size, but lacks most of the head and medial part of the shaft at the proximal end. The smaller humeri, NMC 23020 and 26172, are both complete.

Radio-ulnae - In the collection are two complete left radio-ulnae (NMC 17610 and 29276), and one right radius (NMC 17194) with the distal end of the ulna fused to it.

Carpals - Four left carpals are in the collection. NMC 23018 is a lunate which measures 50 mm long x 39 mm wide x 38 mm thick. NMC 29277 is a scaphoid measuring 60 mm x 39 mm x 46 mm. NMC 26186, an unciform, measures 47 mm x 43 mm x 33 mm. NMC 29278 is most of a cuneiform.

Metacarpals - Two large left metacarpals (NMC 22851, 29272) and a smaller right metacarpal (NMC 20439)

are present. All are complete. The first two fit into the upper limit of group B, while the last is close to the upper limit of group A in the tentatively sexed sample of *Bison crassicornis* (referred) metacarpals from Pleistocene deposits at Gold Run Creek (Harington and Clulow 1973, Figure 48). Therefore, I suggest that NMC 22851 and 29272 represent males, and that NMC 20439 represents a female.

Pelvis - A nearly complete pelvis (NMC 17164) lacks some bone between the obturator foramina, and on the right tuber ischii. The maximum diameter of the right acetabulum is 93.0 mm. Maximum and minimum diameters of the right obturator foramen are 111.4 mm x 71.5 mm. The width across the anterior margins of the acetabula is approximately 320 mm. The maximum anterior width of the pelvis is approximately 560 mm, and its greatest length from the posteriormost part of the ischium to the tuber coxae is 635 mm.

Femora - Two complete specimens are in the collection. NMC 26108, a right femur is much larger than a left one, NMC 22853. The epiphyses are fused to the shaft in both, and probably both represent adults. I suggest that the former represents a male and the

latter a female. Size differences between the sexes in *Bison crassicornis* seem to have been great.

Tibiae - Four complete right tibiae (NMC 26168, 17178, 26167, 26177) vary in total length from 414 mm to 436 mm.

Tarsals - A right calcaneum (NMC 22597) measures 163 mm long x 46 mm wide x 67 mm deep, while a left calcaneum (NMC 22598) measures 175 mm long x 52 mm wide x 68 mm deep. Both are in good condition. A complete left naviculocuboid NMC 26180 measures 76 mm wide x 73 mm deep x 73 mm high.

Metatarsal - A right metatarsal (NMC 20437), lacking the distal epiphysis, probably represents a bison less than 3 years old - approximately the age when the distal epiphysis fuses to the metatarsal shaft in oxen (Silver 1969, p. 286).

Phalanges - Three complete first phalanges (NMC 26182, 17188, 26113) are in the collection from Old Crow Locality 11(1).

On the basis of the skeletal elements preserved,

some of which are not described because of their fragmentary nature, I estimate that at least seven bison are represented at Old Crow Locality 11(1). They include both sexes, and subadult to very old animals.

Discussion

I have found no evidence that *Bison crassicornis* lived in the Yukon Territory before the mid-Wisconsin, although an earlier occupation is likely. No bison fossils are recorded from Unit 2 at Old Crow Locality 44, which is possibly of Sangamon age (>54,000 years B.P.). Radiocarbon dates on bone from seven Yukon large-horned bison specimens range in age from approximately 34,000 years B.P. to about 12,000 years B.P. (Table 5) - almost exactly the same range of dates on *Bison crassicornis* as those from Alaska (Table 6). The species is known from the Dawson, Old Crow and Sixtymile areas, as well as Herschel Island (NMC 17913).

In Canada, apart from the Yukon Territory, probably *Bison crassicornis* occupied parts of the Northwest Territories during the late Pleistocene. Mackay (1958, p. 25) states: "A skull (identified by two palaeontologists, upon the basis of photographs only, as probably that of an extinct bison, *Bison crassicornis*) was picked up from a sand beach 4 miles

{6.4 m} southwest of Tuktoyaktuk. As the skull is not waterworn and is in an excellent state of preservation, it was probably washed out of the sandy bluffs by cliff recession... A former Cape Bathurst trapper has stated that skulls similar to the bison skull of Tuktoyaktuk have been found at Cape Bathurst and from Maitland Point to the mouth of Anderson River." I (Harington 1971a, p. 82) have tentatively ascribed fossils from Baillie Islands, Northwest Territories to *Bison crassicornis*. Two cranial fragments of *Bison crassicornis* have been reported from the Edmonton area, Alberta (Fuller and Bayrock 1965, p. 55, Figures 15-16). The age estimate of 8,000 years B.P. for these specimens may be incorrect (Harington 1971a, p. 76). I have identified a specimen of *Bison crassicornis* (NMC 26050) from late Pleistocene gravels near Edmonton. Although Cowan (1941, p. 45) referred a fifth cervical vertebra from McCulloch Station and the base of a horncore and adjacent frontal bone from Victoria to "*Superbison* cf. *crassicornis*", I think the evidence is too slim yet to infer the presence of *Bison crassicornis* in British Columbia. A fragment of skull with partial horncores from deposits of probable Sangamon age at Fort Qu'Appelle, Saskatchewan, attributed to "*Superbison*" by McCorquodale (1957, p. 42), is best referred to a species

with larger horncores, possibly *Bison latifrons* (Khan 1970, p. 59). I think two specimens of bison from Manitoba are probably referable to *Bison crassicornis*. MMMN P 586 is a cranial fragment with large horncores found in blue clay 16 feet (4.9 m) below the surface at Russell. The other, a posterior cranial fragment from the bed of the Roaring River (Pettipas 1971, p. 8) has horncores in the lower range of *Bison crassicornis*. From a clear photograph, the open sutures on the dorsal surface of the cranium and well developed burrs, suggest it represents a male of the large-horned bison that died in early adulthood.

In the conterminous United States, single crania referred to *Bison crassicornis* are recorded from Kansas, North Dakota and Massachusetts. Lilligraven (1967, pp. 298-299), who reported the specimen from Morris, Kansas, states that, according to its position relative to the Newman Terrace of the Kansas River, it could not be older than early Wisconsin. It should be noted that only one of the two crania from near Zap, North Dakota originally attributed to *Bison crassicornis* (Brophy 1965, p. 214) actually belongs in that species. Specimen 165 (now NDSU Geol. Dept. Z-1) fits the description of *Bison crassicornis*, and bone from it yielded

a radiocarbon date of $7,840 \pm 250$ years B.P. (I-2536) (J.A. Brophy, personal communication 1974), which is the most recent record of the species in North America. Another cranium (formerly Specimen 166, now NDSU Geol. Dept. Z-2) from the same site and approximately the same depth is now referred to *Bison bison occidentalis*. Wood found in close association with the latter specimen gave a date of $5,440 \pm 200$ years B.P. (W-1537). Another highly unusual find was the discovery of a horncore of *Bison crassicornis* in a late Pleistocene deposit at Harvard, Massachusetts (Romer 1951, p. 230). Not only was it peculiar to find a fossil of this species in eastern North America, but this specimen constitutes the first record of an extinct bison from New England! The specimen yielded a radiocarbon date of approximately 21,200 years B.P.

In Alaska, perhaps the oldest record that could refer to *Bison crassicornis* is "*Bison (Superbison) sp.* (large bison)" from the Fox Gravel of possible Kansan age near Fairbanks (Péwé 1975a, Table 11; 1975b, p. 7). Hopkins (Péwé and Hopkins 1967, p. 269) considers that a skull of "*Bison (Superbison) sp.*" was derived from

deposits of possible Yarmouth interglacial age on Baldwin Peninsula. Other specimens designated "*Bison (Superbison)* sp." are reported from beds of Illinoian age near Fairbanks, and from a "forest bed" of Sangamon interglacial age near Tofty (Péwé and Hopkins 1967, p. 268). As no published descriptions of these fossils are available, it is difficult to know whether they should be treated merely as *Bison* sp., or whether they actually represent the large-horned bison, *Bison crassicornis*. Each specimen deserves careful examination. Every effort should be made to determine precisely the species of bison represented by a skull roof with horncores, and a single horncore found in deposits of possible Yarmouth age at Baldwin Peninsula. Evidently *Bison crassicornis* was the commonest large mammal in the Fairbanks area during the Wisconsin glaciation. Of 12 finite radiocarbon dates extending from approximately 32,000 years B.P. to approximately 12,000 years B.P., probably all (I consider "*Bison (Bison) preoccidentalis*" to be a junior synonym of *Bison crassicornis*) refer to *Bison crassicornis*. Therefore, radiocarbon evidence from both the Yukon and Alaska firmly support the idea that large-horned bison lived in Eastern Beringia from

mid-Wisconsin time to 12,000 years ago. Earlier evidence is still tenuous.

Commenting on *Bison crassicornis*, Skinner and Kaisen (1947, p. 190) make an interesting point concerning the relationship between that species and Eurasian bison: "The situation, however, is quite different in Europe where *crassicornis* has not been recognized, but virtually all of the varying segments of the *crassicornis*-like population have been described as distinct species or as subspecies of the loosely defined *Bison priscus*." Later they (Skinner and Kaisen 1947, p. 232) state: "In Eurasia, *crassicornis* apparently ranged over most of northern Russia, Siberia, and down into Europe." They tentatively referred to *Bison crassicornis* the following Eurasian bison: *Bison priscus longicornis*, *Bison priscus fraasi*, *Bison priscus tscherskii*, *Bison priscus deminutus*, *Bison europaeus lenensis*, and *Bison uriformis*. It is important that Eurasian bison be surveyed and analyzed statistically, and that such observations be related to similar data from North American fossil bison.

To summarize, *Bison crassicornis* may have evolved from an ancestor like *Bison alaskensis* (? = *Bison priscus gigas*)

in Beringia, where it was common from approximately Illinoian to late Wisconsin time. It spread westward to Europe during the late Pleistocene, and southeastward from Eastern Beringia through Alberta, possibly Manitoba, North Dakota and Kansas as far as the Atlantic coast of New England about mid-Wisconsin time or earlier. The species may have survived in central North America until early postglacial time (approximately 8,000 years B.P.), while it seems to have become extinct in Eastern Beringia about 12,000 years ago.

During the late Pleistocene, *Bison crassicornis* seems to have been Holarctic in distribution, occupying range from northern Europe through Siberia, Alaska and the Yukon to the North American plains and Atlantic coast. It was the most common ice age bison of northwestern North America. These animals were large in the body and horns compared to living *Bison bison*. They had long hind legs, more like those of the wisent (*Bison bison bonasus*) than the plains bison (*Bison bison bison*) (Figure 77A). A good idea of the appearance of this animal in life can be gained from a well preserved carcass from perennially frozen silt at Dome Creek near Fairbanks, Alaska. The specimen consists of a head complete with hide, horns sheaths, an ear, and the lower part of the body, including four legs with

hooves (Péwé 1975a, Figure 44). Hide and hair from this carcass gave a radiocarbon date of $31,400 \pm 2,040$ years B.P. (ST-1721).

Probably this large-horned grazer preferred cool, loess-steppe or parkland habitat. Human hunters likely exploited this species during the late Pleistocene in the Yukon, as can be seen by examples of incised and spirally-fractured bison bone from the Old Crow Area, and by the posterior part of the bison cranium (probably referable to *Bison crassicornis*) with butcher marks from Sulphur Creek (Dawson Locality 17). Probably wolves and American lions also hunted the large-horned bison.

Bison bison occidentalis (western bison)

Western bison remains (Table 92) are about as rare as those of Alaskan bison (*Bison alaskensis*) in Yukon Pleistocene deposits. Two specimens from the Dawson Area are described. This species has been reported previously from the Yukon Territory on the basis of a single fragmentary cranium (USNM 2643), which was collected by Maddren on the Old Crow River in 1904 (Gilmore 1908, p. 34, Plate XII). I consider that nominal identifications of other crania from the Dawson Area (e.g. "*B. occidentalis*" (Gilmore 1908, p. 34) and "*Bison (occidentalis?)*" (Quackenbush 1909, p. 91)) are questionable.

Table 92. Measurements of Pleistocene western bison (*Bison bison occidentalis*) crania from the Yukon Territory compared to those from Alberta and other parts of North America, and to crania of *Bison bison antiquus* from southern North America.

SPECIMENS	SEX	ESTIMATED AGE	MEASUREMENTS (mm) *																													
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Bison bison occidentalis.</i> Pleistocene, Y.T.																																
NMC 2242 Dominion Ck. (Dawson Area)	♂	Adult	767	804	295	360	272	107	114	342	270	140	75	105	148	322	307	-	-	-	-	-	-	-	-	-	-	-	132	94	86	96
NMC 17333 Dawson Loc. 5	♂	Adult	775	790	315	377	284	100	111	329	284e	136	73	109	150	278	288	-	-	-	-	-	-	-	-	-	-	-	133	90	96	109
<i>Bison bison occidentalis.</i> Pleistocene, Alta.																																
NMC 12442 Athabasca	♂	Adult	858	870	275	335	257	95	104	318	275e	140	72	110	152	354	294	348	251	-	-	-	-	-	-	-	-	-	130	91	86	94
<i>Bison bison occidentalis.</i> Pleistocene, N. America (Skinner and Kaisen 1947, Table 12)																																
M	♂♂	Adult	747	782	279	340	243	91	98	290	275	131	-	-	158	-	299	351	-	187	115	147	91	153	516	-	493	259	140	93	97	95
OR			670- 875	735- 892	222- 330	275- 405	210- 290	76- 100	85- 114	253- 336	259- 307	124- 147	-	-	136- 177	-	277- 340	328- 400	-	169- 204	102- 125	137- 160	84- 102	143- 168	467- 582	-	471- 543	229- 273	121- 169	86- 104	85- 110	83- 112
N			13	8	12	12	11	16	16	16	9	8	-	-	6	-	12	8	-	5	6	6	5	5	6	-	5	8	11	16	12	9
<i>Bison bison antiquus.</i> Pleistocene, N. America (Skinner and Kaisen 1947, Table 14)																																
M	♂♂	Adult	881	-	281	336	245	98	107	320	-	-	-	-	-	-	319	353	-	205	-	-	-	-	545	-	510	295	138	93	88	89
OR			816- 975	-	220- 344	280- 395	197- 280	90- 108	92- 122	290- 358	-	-	-	-	-	-	292- 357	346- 360	-	188- 218	-	-	-	-	520- 560	-	482- 527	240- 350	128- 147	83- 108	68- 100	66- 114
N			10	-	13	10	8	14	13	14	-	-	-	-	-	-	12	2	-	4	-	-	-	-	3	-	4	11	8	13	12	10

* See measurements with Table 86.

I wish to inject a note of doubt at this point. On the basis of the Yukon and Alberta specimens I have examined, I believe it is arguable whether they should be considered as *Bison bison occidentalis* or *Bison bison antiquus*. They approach the latter subspecies (using definitions of Skinner and Kaisen 1947) in that their horncores are not strongly backswept, and the former subspecies in the relative narrowness of their skulls at the constriction between horncores and orbits. In some of these specimens, the horncores rise well above the frontal plane (e.g. NMC 2242, 17333) as in the former subspecies, and in others (e.g. UA* 600), like the latter subspecies, they do not rise above the frontal plane. These specimens have neither sharp, back-twisted horncore tips (said to characterize *occidentalis*) nor very blunt, straight ones (said to characterize *antiquus*). Horncore indices of curvature and compression are virtually the same in *occidentalis* and *antiquus*; however horncore indices of proportion and length are higher on the average in *occidentalis*. In the index of proportion, NMC 2242 from Dominion Creek and NMC 12442 from Athabasca, Alberta are closest to *antiquus*, while NMC 17333 from Eldorado Creek is closest to *occidentalis* (Table 92). In the index of length, both Yukon specimens and the Athabasca specimen (NMC 12442) are closest to *occidentalis*. Ultimately, for

practical purposes, it may be best to consider all *occidentalis* and *antiquus* specimens as belonging to a single subspecies *Bison bison antiquus* (which has priority), which had its origins in Beringia. Largely as a matter of convention, because the specimens described here are northern bison, I refer them to *Bison bison occidentalis*.

Referred specimens

NMC 2242 is from the upper part of Dominion Creek in the Dawson Area (exact locality unspecified). A note with the NMC catalog states that it was identified in 1947 as *Bison preoccidentalis* by M.F. Skinner. However, I think it is a much better fit for "*Bison occidentalis*" according to measurements of that species provided by Skinner and Kaisen (1947, Table 12). Again, I emphasize the value of Skinner and Kaisen's horncore indices for comparative purposes - while keeping relative sizes in mind, of course. The specimen is a posterior cranial fragment with rather short, stubby horncores compared to those of *Bison crassicornis*. The fossil lacks bone anterior to the orbits. The dorsal part of the right orbit is present: the left orbit is missing. The frontal region is slightly concave between the horncore bases. The horncores are neither depressed near their bases nor strongly backswept as in most *Bison crassicornis* crania, but

extend laterally almost perpendicular to the cranial axis - approaching *Bison bison antiquus* in this respect. Approximately 27 mm left of the frontal suture, between the horncores, there is a 15 mm long aperture with signs that it was a healed or partly healed wound. Perhaps the opening was made by the tip of the horn of another bison during a fight in the rutting period, or by the weapon of an early human hunter. The fossil is stained brown, being darker than NMC 17333. It seems to be heavily permineralized.

NMC 17333 from Dawson Locality 5 is a posterior cranial fragment with horncores. The tip of the right horncore is slightly damaged. The specimen lacks bone anterior to the orbits. The dorsal part of the left orbit is preserved, whereas the right orbit is missing. Basicranial and occipital regions are damaged. The occipital condyles have been heavily eroded. According to G. Franklin, who collected the specimen, it was derived from muck just above the gold-bearing gravel. The specimen is pale buff and may be of late Wisconsin age. I intend to obtain radiocarbon dates on bone from these specimens in an attempt to determine approximately the time of origin of this subspecies, which seems to have stemmed from *Bison crassicornis* in

Beringia during the late Wisconsin.

Discussion

In Canada, apart from the Yukon, *Bison bison occidentalis* is known from Alberta, Manitoba, and possibly the Northwest Territories. B. Gordon (personal communication 1969) mentioned the discovery of a large "*Bison antiquus*" skull from near Nahanni Butte in the Northwest Territories. Knowing the possible confusion between the subspecies, the Nahanni specimen may well belong with the fossils described here. NMC 12442 (Table 92) is a posterior part of a cranium with complete horncores from near Athabasca, Alberta. The fossil was derived from 15 feet (4.6 m) below the surface of terrace gravels. It is very similar to the Yukon specimens and two other *Bison bison occidentalis* skulls that were probably derived from terrace gravels approximately 8,000 years old at Edmonton, Alberta (Fuller and Bayrock 1965, p. 56; Harington 1976 MS., p. 30). In Alberta other *Bison bison occidentalis* fossils are known from late Wisconsin gravels at Empress ("*Bison* cf. *occidentalis*"), Cochrane (approximately 11,000 years old) and Taber, and from early postglacial deposits near Three Hills (approximately 9,600 years old) (Harington 1976 MS., pp. 29, 32, 42). In Manitoba,

Bison bison occidentalis crania have been collected from early postglacial deposits near Treesbank, and other fossils possibly belonging to this subspecies were found near Douglas (Pettipas 1971, p. 9).

In the conterminous United States, *Bison bison occidentalis* remains have been reported from Montana (Rasmussen 1974, p. 59), Wyoming (Wilson 1974b, p. 96), Minnesota, Nebraska, Kansas, Iowa, Texas and possibly California (Skinner and Kaisen 1947, pp. 172-173).

The holotype (USNM 4157) of *Bison bison occidentalis* is from Fort Yukon, Alaska, which is not far from the Alaska - Yukon border. Another specimen from Tatlo River, Alaska has been referred to this subspecies by Skinner and Kaisen (1947, p. 172).

In Siberia, relatively small-horned, *occidentalis*-like bison appeared toward the end of the last glaciation (Flerov and Zablotski 1961), where the transition from small *Bison crassicornis* (= "*Bison priscus crassicornis*") to *Bison bison athabasca* (= "*Bison priscus athabasca*") evidently occurred (Sher 1971, p. 209). This transition seems to have happened simultaneously in the eastern and western parts of Beringia.

In summary, *Bison bison occidentalis* probably evolved in Beringia. Evidently it arose from *Bison crassicornis* toward the close of the Wisconsin glaciation and had reached the eastern flanks of the Cordillera in southern Alberta (e.g. Cochrane) approximately 11,000 years ago, having spread southward via the "western corridor". Western bison apparently reached maximum numbers some 9,000 to 8,000 years ago in western North America. This subspecies can be recognized in deposits as late as 6,500 years old in Wyoming (Wilson 1974b, p. 96) and approximately 5,600 years old in Iowa (Hall 1972, p. 604). By that time (the hypsithermal), most herds of *Bison bison occidentalis* had undergone the transition to wood bison (*Bison bison athabasca*) in the north, while southern herds had adapted to the prairie environment, becoming plains bison (*Bison bison bison*).

Bison bison occidentalis was Holarctic in distribution, ranging from eastern Siberia through Alaska and the Yukon to southwest-central North America during the late Wisconsin and early postglacial.

Likely the western bison was close in appearance to the modern wood bison, but it may have been a little larger. As *Bison bison occidentalis*

seems to have been in a transition from a steppe-adapted bison to a woodland-adapted form, I speculate that it was in the process of accommodating to life in moister, more heavily wooded regions, such as the margins of subalpine forests, open forest and parkland. Analyses of pollen and mollusc shells associated with a complete, articulated skeleton of *Bison bison occidentalis* from a peat bed near Marion, Iowa support this contention. Pollen of oak and elm represent 54% and grass pollen represents 3% of the pollen sampled near the skeleton. Remains of snails (*Carychium exiguum*, *Carychium exile*, *Hawaia minuscula*, *Strobilops labyrinthica* and *Triodopsis multilineata*) associated with the skeleton are typical elements of the present terrestrial molluscan fauna found in protected wooded areas of eastern Iowa (Hall 1972, pp. 604-606). I had the opportunity to examine and make a stratigraphic section of the locality near Treesbank, Manitoba that produced a number of *Bison bison occidentalis* cranial and postcranial specimens over the period 1915-1967 (Hay 1924, p. 200; Harington, Field Notes 1967II, pp. 23-24). I found bison material *in situ* (17 feet (5.2 m) below the surface in a gray, highly organic, sandy clay unit) near a log

1.4 feet (0.5 m) in diameter. Much leaf matter was compacted under the log and the fossiliferous unit contained many twigs. Wood from this unit yielded a radiocarbon date of $9,100 \pm 110$ years B.P. (Y-415). Evidently western bison occupied this area during the early postglacial when it was wetter and more heavily wooded than at present.

As a hypothesis for testing, I suggest that:

(a) the hypsithermal (approximately 7,000 to 5,000 years B.P.) placed relatively great, and sudden stress on the herds of western bison that were best adapted to woodland or parkland conditions; (b) that some of the herds were able to adapt to life on the arid plains (*Bison bison bison*), which entailed a good deal of morphological and behavioral change; and (c) that other herds withdrew northward and westward following the retreating margins of the boreal and subalpine forests, or remained in those parts of northern and western North America (*Bison bison athabasca*), retaining the basic form (except for smaller horncores) and habits of their ancestors.

Like other bison, this subspecies probably fed mainly on grasses, forbs and sedges. Its fossils could be useful paleoenvironmental indicators of rather moist, partly wooded terrain. Wolves were undoubtedly a common predator of western bison. People are known to have

hunted these bison (e.g. Hawken Site, Wyoming, where skeletal remains were associated with side-notched points (Wilson 1974b, p. 96), and the Bayrock Site near Taber, Alberta, where a cobble chopper was found embedded in the braincase of an *occidentalis* cranium (Wormington and Forbis 1965)).

Bison bison athabasca (wood bison)

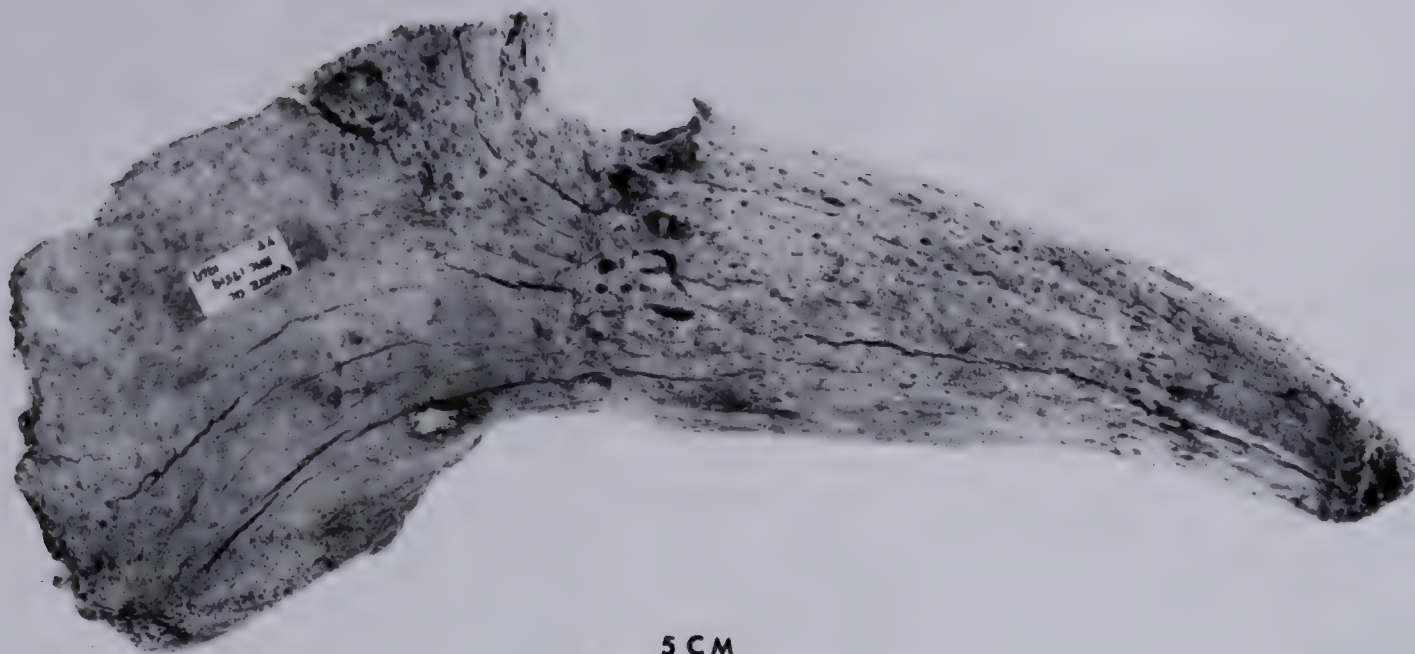
A single specimen of the wood bison (Figure 80A-C, Table 93) was collected at Quartz Creek in the Dawson area in 1969. Despite its relatively recent age, it is described here because it helps to round out the history of bison in the Yukon Territory. Evidently this subspecies was the last bison to occupy Eastern Beringia under natural conditions. Two other specimens of *Bison bison athabasca* have been recorded from the Yukon Territory by Skinner and Kaisen (1947, p. 167). In 1904, Preble collected a cranium with horncores and orbits (USNM 16861) from the Peel River, and a year later Sheldon picked up an "unfossilized" cranium with horncores (USNM 5513) from a locality 12 miles (19 km) upstream from the mouth of Pelly River.

Referred specimen

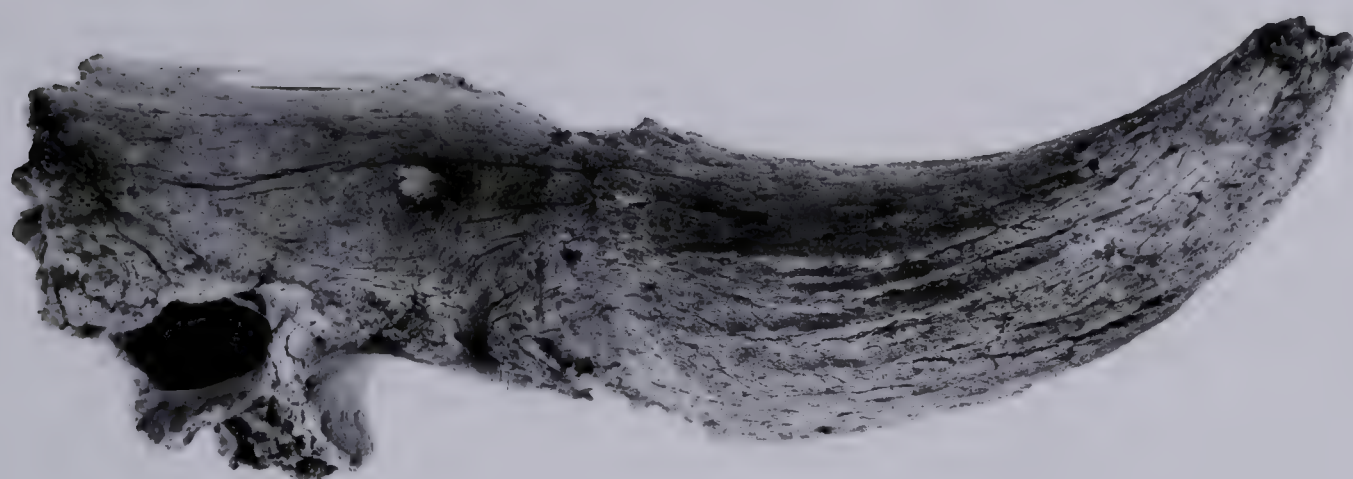
NMC 17519 from Dawson Locality 6 consisted of

Figure 80. Right horncore lacking tip with attached cranial fragment (NMC 17519, Dawson Locality 6) of a postglacial wood bison (*Bison bison athabasca*). Bone from this specimen has yielded a radiocarbon date of $1,350 \pm 95$ years B.P. (I-5404).

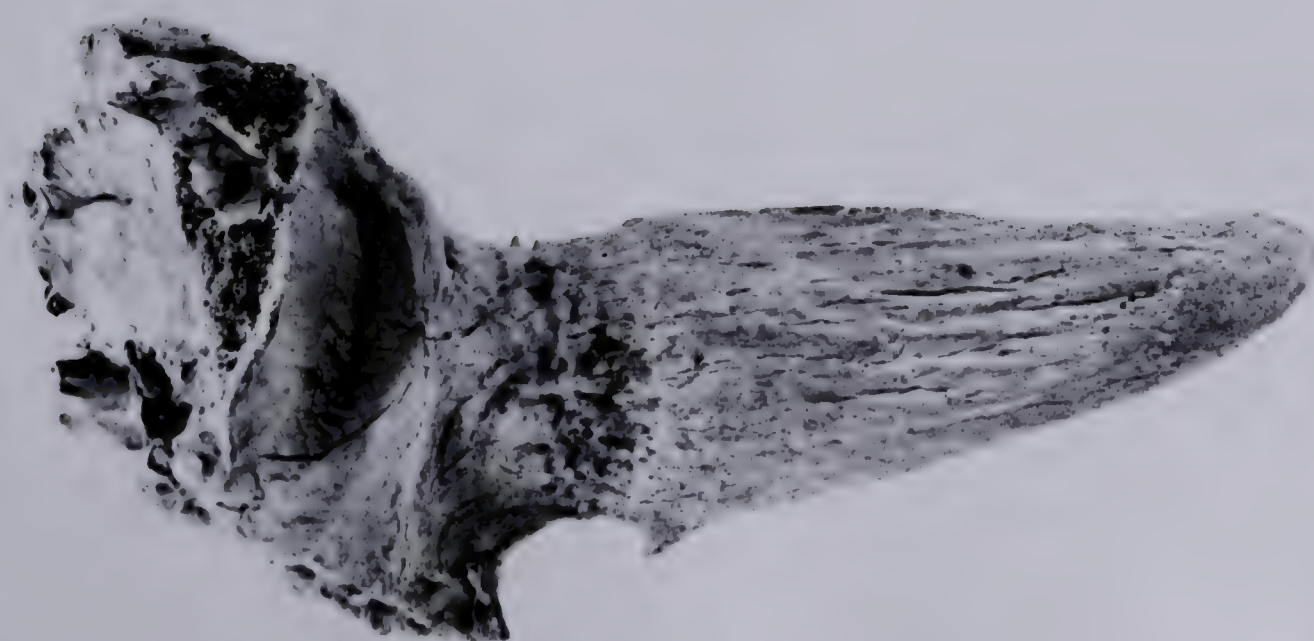
- A. Dorsal view.
- B. Posterior view.
- C. Ventral view.



A



B



C

Table 91. Measurements of a postglacial wood bison (*Bison bison athabascus*) horncore from the Yukon Territory compared to horncores from Recent North American wood bison.

SPECIMENS	SEX	ESTIMATED AGE	MEASUREMENTS (mm) *																														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	
<i>Bison bison athabascense</i> . Postglacial, Y.T.																																	
SMC 17519 Dawson Loc. 6	♂	Adult	-	-	208e	250e	196e	77	75	244	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	128e	103	85	-
<i>Bison bison athabascense</i> . Recent, North America (Skinner and Kaisen 1947, Table 11)																																	
M		Adult	665	683	216	255	189	85	92	271	263	130	-	-	149	-	288	355	-	195	121	148	92	160	537	-	477	271?	135	92	80	75	
OR			585- 736	645- 750	155- 260	190- 290	150- 200	72- 97	81- 108	230- 300	185- 296	113- 140	-	-	140- 159	-	272- 312	326- 384	-	179- 204	108- 130	143- 158	-	151- 170	525- 555	-	447- 507	248- 286?	126- 149	84- 98	62- 92	57- 52	
N			9	5	9	8	7	8	8	9	7	7	-	-	6	-	9	4	-	3	3	3	2	3	3	-	3	5	7	8	9	9	

* See measurements with Table 86.

a right horncore attached to part of the right frontal. The horncore is deeply grooved, except on its dorsal surface. Matrix in crevices near the burr suggests that the specimen was derived from a silty peat deposit. The specimen is grayish in color. The pedicel and horncore are preserved, while the remainder was sacrificed to obtain a radiocarbon date. The bone yielded a date of $1,350 \pm 95$ years B.P. (I-5404), which may be close to the time when wood bison last occupied the Yukon Territory.

Discussion

In Canada, apart from the Yukon, herds of wood bison may still survive in Wood Buffalo Park near Great Slave Lake in the Northwest Territories. It is questionable that they are pure *Bison bison athabasca*, because, during helicopter surveys of the range, L.P.E. Choquette (personal communication 1973) informed me that he saw trails connecting the habitat of the supposedly isolated herd of wood bison with the range of mixed herds of wood and plains bison farther south. Wood bison remains have been reported from Lake Athabasca (Skinner and Kaisen 1947, p. 166), Alberta. I have identified a skull with horncores collected by R. Moore near Rumsey, Alberta, and other cranial fragments with horncores from national parks on the border of Alberta and British Columbia.

Banfield (1958) states that wood bison occurred in Banff National Park until 1858, when apparently the last individual was killed in Pipestone Valley. Soper (1964, p. 376) comments that wood bison were found in suitable areas throughout northern Alberta. They formerly occupied the extreme northern parts of British Columbia. A Recent skull was found in muskeg near Atlin. Either the wood or the plains bison was common in grasslands along the Peace River, but the last of them were shot near Fort St. John, British Columbia in 1879 (Cowan and Guiguet 1965, p. 388).

In the conterminous United States, specimens of wood bison are recorded from Wyoming, Utah, Oregon and Colorado (Skinner and Kaisen 1947, pp. 167-168).

Two specimens have been identified from Alaska. An "unfossilized" cranium with horncores was collected near St. Michael near Norton Sound in the west, and a complete unweathered skull was found in a cut bank of a creek 30 miles (48 km) upstream from the mouth of the Tanana River in central Alaska (Skinner and Kaisen 1947, p. 167).

In the Kolyma Lowland of northeastern Siberia,

Sher (1971, p. 209) states that a skull, from deposits dating to the close of the last glaciation or the beginning of the postglacial on the Bolshaya Chukochya River, corresponds to the wood bison "*Bison priscus athabasca*" (= *Bison bison athabasca*). Could wood bison have evolved simultaneously from the same basic *occidentalis* stock in both Siberia and North America? It is important to ascertain with precision the identifications and geological ages of the earliest wood bison in Siberia and North America to answer this question.

In North America, I speculate that *Bison bison athabasca* arose from *Bison bison occidentalis* on the forest and parkland margins west and north of the plains that were becoming arid during the hypsithermal (which lasted from approximately 7,000 to 5,000 years B.P.). Wood bison were distributed from western Alaska to the Yukon, and south along the eastern flanks of the Cordillera from northern British Columbia and the western Northwest Territories to Colorado. Possibly increasing depths of snow, altering vegetation patterns, and human hunting in these areas from late postglacial to historic times resulted in decimation of these animals except in favorable habitat near Great Slave Lake, where a herd of approximately 200 pure, or nearly pure wood bison survives. This range is

characterized climatically by long, cold winters, short hot summers and little precipitation, nearly half of which falls as snow (Fuller 1962, p. 11).

Wood bison are similar in appearance to plains bison (*Bison bison bison*), but are generally larger and darker. In addition, they have longer, more robust horns and broader skulls. This subspecies stands about 5.7 feet (1.7 m) high at the shoulder and weighs up to 2,400 pounds (1,089 kg). Wood bison are gregarious, have keen senses of vision and smell, and are good swimmers. Occasionally violent fights occur between bulls during the rutting period, the peak of which occurs in mid-August. They prefer heavy mixed wood forest with scattered grasslands and ponds or lakes. In Wood Buffalo Park, small, scattered herds range over extensive areas of spruce - poplar forest, sandy pine ridges, meadows and patches of grassy uplands. In November and May they migrate from wooded hills to the Peace River valley, a distance of up to 150 miles (241 km). Intersecting trails, sand wallows, rubbing trees and water holes mark the favored parts of their range. Forage consists of sedges, grasses and forbs. In addition to human hunters, wolves, brown bears and occasionally mountain lions prey on, or may have preyed on wood bison (Soper 1941, Fuller 1962, Banfield 1974).

Soergelia cf. *elisabethae* (Soergel's muskox)

Several cranial and postcranial specimens from Pleistocene deposits of the Yukon Territory are referable to the genus *Soergelia* (Figures 81A-B, 82A-B, Tables 94-95). This genus has been described as a member of the Caprinae (Schaub 1951, p. 376) and has been informally called a steppe goat ("Steppeziegen") (Toepfer 1963, p. 156), but I agree with C.E. Ray (personal communication 1973) that it should be called a muskox, because of "the finely and uniformly vesicular structure of the horn cores throughout most of their length, in contrast to the more irregularly and coarsely vesicular or vacuous, truly 'cavicorn' structure of caprines; and the typically ovibovine, not caprine, dentition." I would also add that the horncores, if bent down by the cheeks, would look very much like those of the living tundra muskoxen (*Ovibos moschatus*). Furthermore, except for their relative slenderness, the metacarpals of *Soergelia* are remarkably like those of *Ovibos*.

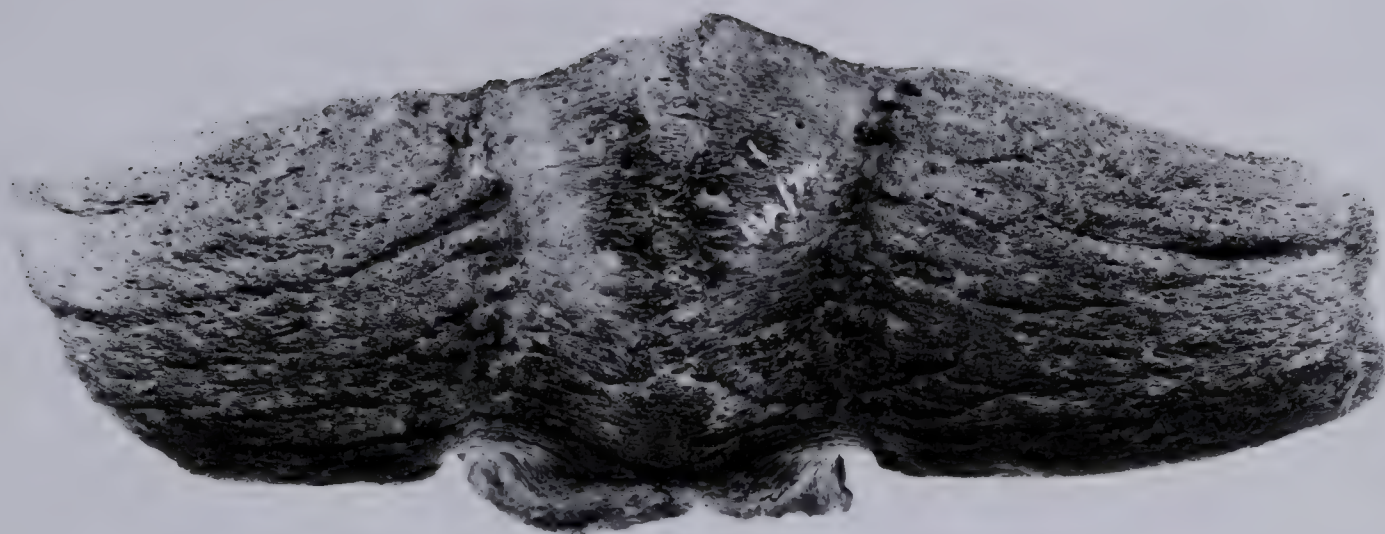
Soergel's muskoxen are interesting and important because their fossils extend in a chain from Europe, through Siberia and the Yukon, to Kansas and Texas. I present evidence that specimens of this genus are index



Figure 81. Posterior cranial fragment with partial
horncores (NMC 13601, Old Crow Locality 11A)
of a Pleistocene Soergel's muskox
(*Soergelia* cf. *elisabethae*).

A. Dorsal view.

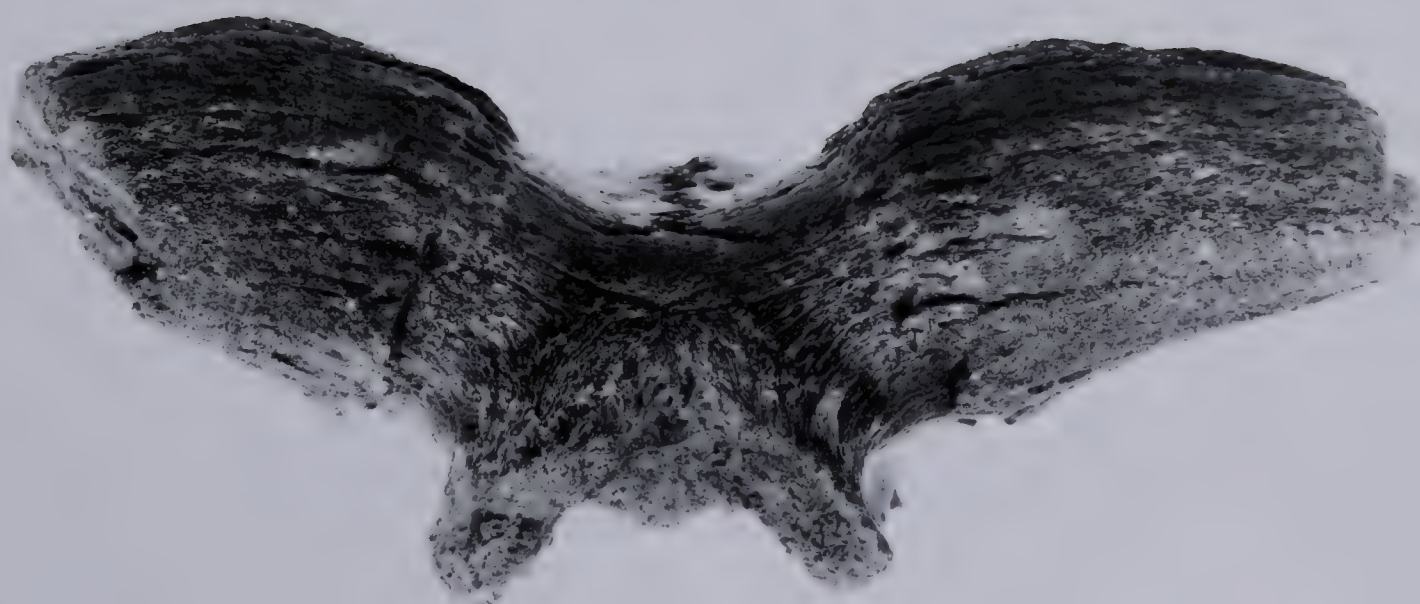
B. Posterior view.



5 CM

A

5 CM



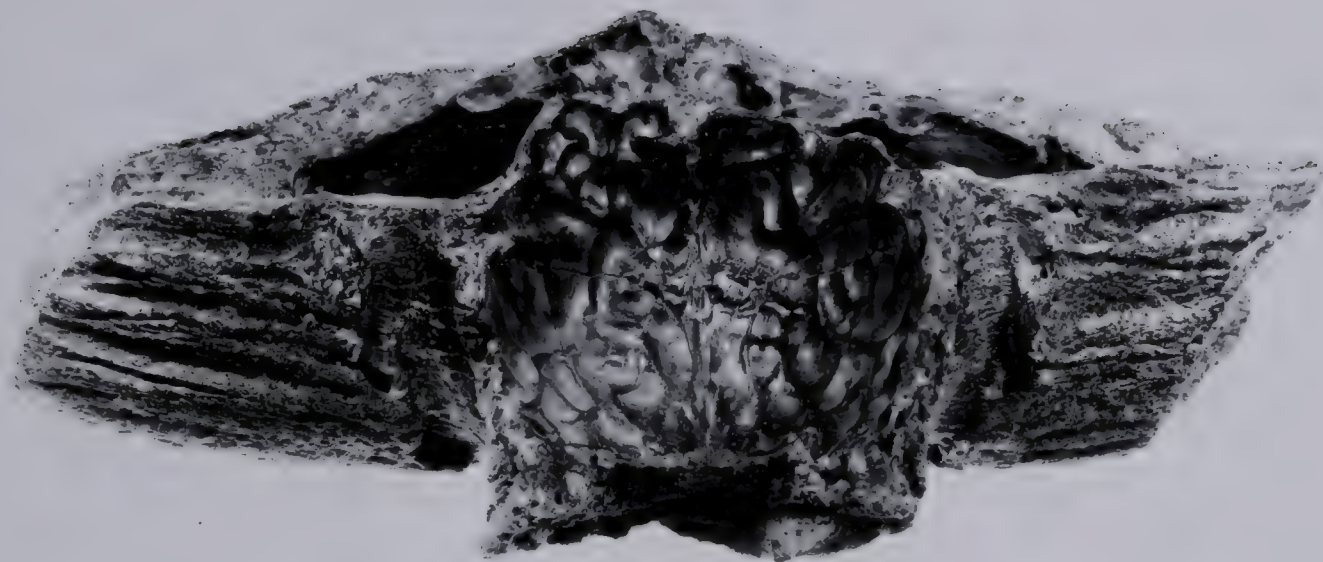
B



Figure 82. See Figure 81. Posterior cranial fragment with partial horncores (NMC 13601, Old Crow Locality 11A) of a Pleistocene Soergel's muskox (*Soergelia* cf. *elisabethae*).

A. Ventral view.

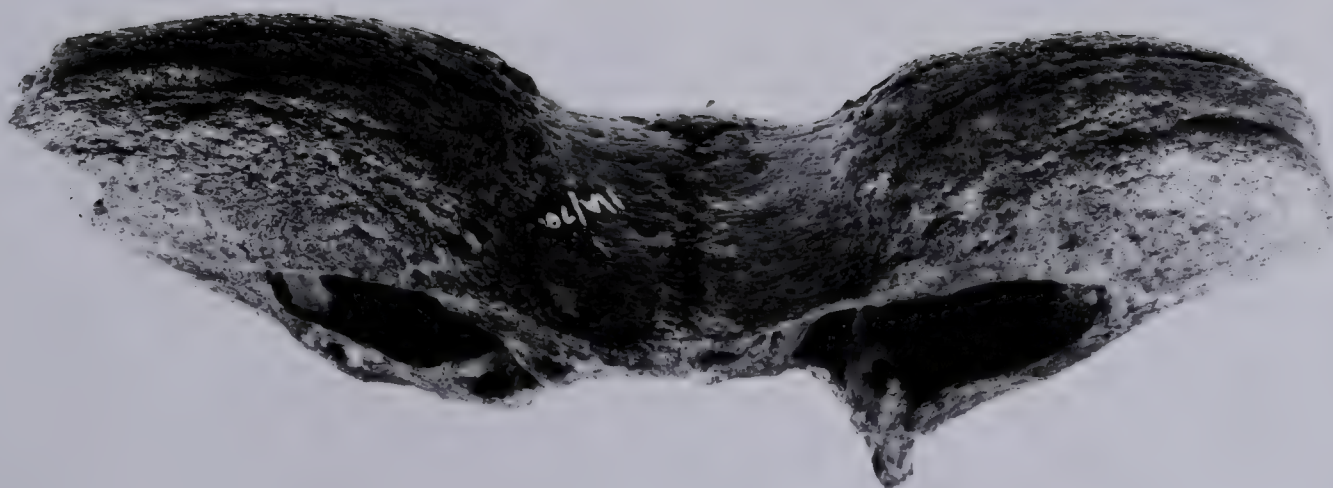
B. Anterior view.



5 CM

A

5 CM



B

Table 94. Measurements of Pleistocene Soergel's muskox (*Soergelia* cf. *elisabethae*) crania and horncores from the Yukon Territory compared to those of *Soergelia elisabethae* from East Germany, *Soergelia* sp. from Siberia and *Soergelia* cf. *elisabethae* from Texas.

Specimens	Measurements (mm)*								
	1	2	3	4	5	6	7	8	9
<i>Soergelia</i> cf. <i>elisabethae</i> , Pleistocene, Y.T.									
NMC 13601 Old Crow Loc. 11A	61.5	90.0	70.4	85.9	250.0e	79.3	-	-	27.5
NMC 23209 Old Crow Loc. 11A	-	-	56.1	62.3	188.0	-	129.0	186.0	-
NMC 20603 Old Crow Loc. 20	-	-	58.6†	-	-	-	-	178.0	28.0e
<i>Soergelia elisabethae</i> , Pleistocene, E. Germany **									
NMC 30502 (plaster cast of Weimar 1967/8991 = Mus. Basel D459) Rastenberg area	74.5	96.0	64.4	76.5	231.0	73.5	160.0e	184.0e	32.0
<i>Soergelia</i> sp. Pleistocene, Siberia ***									
NMC 31020 (plaster cast) Chukochya R. "OKC-157" "OKC-154" Uncataloged cast Bobrovka-Irtysh region	77.7	90.4	64.3	77.8	219.0	96.2a	140.0	167.0	28.6
	-	-	60.8a	82.4	235.0	-	-	-	-
	-	-	51.4	70.4	199.0	-	-	-	-
	-	-	-	81.4†	-	-	-	-	-
<i>Soergelia</i> cf. <i>elisabethae</i> , Pleistocene, Texas. (Troxell 1915, p. 481)									
YPM 10920 Rock Creek	75.0	-	85.0	74.0	-	92.0	-	-	-

* 1 - Minimum distance between horncore burrs across frontals.

2 - Distance between horncore burrs at posterior margin.

3 - Vertical diameter of horncore at burr.

4 - Transverse diameter.

5 - Circumference of horncore at burr.

6 - Minimum width at cranial constriction posterior to horncores.

7 - Length of horncore on inner (anterior) curve.

8 - Length of horncore on outer (posterior) curve.

9 - Thickness of braincase between anterior margins of horncore bases.

** I am grateful to Dr. H.D. Kahlke of the Institut für Quartärpaläontologie, Weimar, East Germany for supplying this cast.

*** I am grateful to Dr. A.V. Sher of the Paleontological Institute, USSR Academy of Sciences, Moscow for supplying this cast.

Table 95. Measurements of Pleistocene Soergel's muskox (*Soergelia* cf. *elisabethae*) metacarpals from the Yukon Territory compared to those of *Soergelia elisabethae* from East Germany and *Soergelia* sp. from Siberia.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Soergelia</i> cf. <i>elisabethae</i> .Pleistocene, Y.T.							
NMC 20757 Old Crow Loc. 29	176.8	51.5	31.9	31.7	21.2	57.1	31.5
NMC 20137 Old Crow Loc. 74	-	-	-	-	19.0a	55.7	29.9
<i>Soergelia elisabethae</i> .Pleistocene, E. Germany							
Süss. 1965/2568 (cast) Süssenborn	180.6	49.3	33.3	30.7	22.9	55.4	29.9
<i>Soergelia</i> sp. Pleistocene, Siberia							
"KCC-5"	168.9	48.0	30.0	30.7	19.8	53.5	27.3
"OCK-73-752"	170.6	50.9	29.2	30.8	22.2	55.5	27.4
"CH-30"	181.5	49.9 [†]	30.2	30.0	21.3	59.3	30.2
"S-100-329"	-	51.6	31.6	-	-	-	-

* 1 - Total length.
2 - Proximal width.
3 - Proximal depth.
4 - Midshaft width.
5 - Midshaft depth.
6 - Distal width.
7 - Distal depth.

fossils that provide support for cross-continental correlation of deposits of Kansan age in North America, with those of Mindel or Elster age in Eurasia. So far, the only remains of *Soergelia* from northern North America are from sediments in the Old Crow Basin of the Yukon Territory.

Referred specimens

NMC 13601 from Old Crow Locality 11A is an upper, posterior portion of a cranium, with horncores that lack the distal halves. The anterior parts of the frontals and horncores (near their bases) are missing. The specimen has the following characteristics of *Soergelia elisabethae*: (a) longitudinally-grooved horncores that rise laterally and forward; (b) horncores with well-defined burrs, which are separated across the frontals by a space of 60 to 80 mm; (c) solid horncores, except for large pneumatic cavities near their bases. It should be noted that the horncores of NMC 13601 are slightly lower set and more massive than those of *Soergelia elisabethae* from East Germany (NMC 30502 - cast) and *Soergelia* sp. (NMC 31020 - cast) from Siberia. The great age of the individual is indicated by the tightly fused (although somewhat eroded) sutures. NMC 13601 probably represents an old male. The grooving, which parallels the length of the horncore, is rather deep and coarse on the ventral surface

compared to the dorsal surface. Details of the bone adjacent to the upper surface of the brain are well preserved. The fossil is blackish brown in color, and seems to be deeply permineralized by iron oxide.

Apart from the slight downward deflection of the horncore about 50 mm from the burr, NMC 13601 is closer to *Soergelia elisabethae* (NMC 30502 - cast) from East Germany than *Soergelia* sp. (NMC 31020 - cast) from Siberia, and it is referred to *Soergelia* cf. *elisabethae*.

NMC 23209 from Old Crow Locality 11A is a short, complete left horncore with a small part of the adjacent cranial bone attached. It is more like horncores of NMC 31020 from Siberia in size, but it curves gradually forward rather than being flexed forward, attenuating rapidly, about 4 cm from the burr. It may represent a female or a subadult male. The large pneumatic cavity at the base of the horncore and the details of the surface sculpture are clearly seen. The fossil is stained brown.

NMC 20603 from Old Crow Locality 20 consists of most of a right horncore with an attached frontal fragment. The proximal two-thirds of the anterior surface

is lacking. Except for its paler color, it is similar to NMC 23209, and it may represent a female or subadult male.

I suspect that the Siberian form belongs to a new species of *Soergelia*, because all five of the specimens I have examined from Siberia are more sharply tapered in their distal two-thirds than any other *Soergelia* that I have seen. All but one ("OKC-100") are bent forward more strongly in their distal portion than in the specimen of *Soergelia elisabethae* from near Rastenberg, East Germany, or than in NMC 23209 from the Yukon Territory.

Two metacarpals are referred to *Soergelia* cf. *elisabethae*. They look very much like *Ovibos* metacarpals, except they are more slender. NMC 20757 from Old Crow Locality 29 is a complete left metacarpal. It matches well the cast of a right metacarpal of *Soergelia elisabethae* (Süss. 1965/2568) from Süssenborn, East Germany, and is close in size to "CH-30" from Siberia. It is worth noting that Siberian *Soergelia* metacarpals "KCC-5" and "OCK-73-752" are similar in shape to other *Soergelia* metacarpals, but average approximately 10 mm less in total length. Perhaps they represent females,

while the remainder have been derived from males. The deep foramen in the central part of the proximal articular surface of NMC 20757 and the posterior channel leading to it, match those features on "S-100-329", the proximal half of a right metacarpal from Siberia. The Yukon fossil is stained dark brown, and has patches of iron oxide adhering to its surface. NMC 20137 from Old Crow Locality 74 is the distal third of a right metacarpal. It is like the distal end of NMC 20757 in every detail, except that it is slightly smaller and is stained black.

Discussion

There is no evidence of the geological age of these specimens, except that their dark staining indicates a pre- late Wisconsin age. Stratigraphic and paleo-environmental evidence from *Soergelia* fossils found *in situ* elsewhere strongly suggests that the Yukon fossils are of Kansan age. Although *Soergelia* has not been reported from other parts of Canada, perhaps muskox ("Ovibovini") material from deposits considered to be of late Aftonian age at Wellsch Valley, Saskatchewan (C.S. Churcher, personal communication 1975), may be referable to one of the high-horned muskoxen, such as *Euceratherium* or *Soergelia*.

In the conterminous United States, a partial

cranium from deposits of late Kansan age at Rock Creek, Texas was described as *Preptoceras mayfieldi* (YPM 10920) (Troxell 1915b, p. 479). C.E. Ray and I examined this specimen next to a cast of *Soergelia elisabethae* from East Germany, noticing only a few small differences between them. Consequently, I suggest that YPM 10920 is referable to *Soergelia* cf. *elisabethae*. In the summer of 1973, R.E. Eshelman (personal communication 1973) collected the posterior part of a cranium with half of the left horncore, all but the tip of the right horncore, and most of the occipital region from deposits of approximately late Kansan age in Cloud County, Kansas. From three clear, scaled photographs of the specimen, I tentatively refer it to *Soergelia* cf. *elisabethae*. It appears to differ little from the best East German cranial fragments. To my knowledge, it is the most complete cranial fossil of *Soergelia* discovered.

No *Soergelia* remains have been reported from Alaska, but, as specimens are known from northeastern Siberia and the Yukon Territory, it is reasonable to predict that they will be found eventually in Alaska.

When I visited Moscow in 1973, A.V. Sher kindly allowed me to examine and measure most of the specimens

of *Soergelia* collected from Siberia to that time. The collection consisted of a dorsal posterior cranial fragment with nearly complete horncores, four horncores or horncore fragments (one was a cast), two cheek teeth, a magnum, three metacarpals and the proximal half of another, and the proximal half of a metatarsal. Some of these specimens are from the Olyor Suite of Mindel (?Kansan) age in the Kolyma Lowlands of northeastern Siberia (Sher 1971, pp. 233-235). The cast of a relatively large horncore with attached frontal and parietal bone, represents a specimen collected from Pavlodarsk-on-the-Irtysh in the southern part of western Siberia. A metatarsal fragment is known from the Kuznets Basin farther west (Sher 1971, p. 233). These fossils seem to be of similar age to those from the Olyor Suite (i.e. they belong to the Tiraspol faunistic complex (Gromov 1948)).

Soergelia remains were first reported from Europe (Soergel 1939, Schaub 1951). Kahlke (1969, pp. 543-544) discusses *Soergelia* fossils from four European localities: from gravels at Kapellenberg, a hill near Rastenberg, East Germany (German Democratic Republic) of probable early Elster (?early Kansan) age; from gravels at Süssenborn near Weimar, East Germany of

early Elster (?early Kansan) age; from a fissure filling at Zlatý Kun near Koneprusy, Czechoslovakia of Mindel II (?late Kansan) age; and from fluvial and lacustrine deposits at Oltenia, Roumania of middle Pleistocene ("end of Cromer and Mindel") (?Kansan) age. All of these specimens are referred to *Soergelia elisabethae* by Kahlke (1969, p. 543) except for the metatarsal fragment from Oltenia, which is best referred to *Soergelia* sp.

I speculate that *Soergelia* evolved from a relatively small, very high-horned muskox belonging to the *Euceratherium* (including *Preptoceras*) - *Boöpsis* group in northern Asia prior to the Kansan glacial. The zoogeographic and geochronological evidence amassed so far presents a remarkably cohesive picture, indicating a rapid Holarctic dispersal of *Soergelia* in Kansan time - westward to Roumania, Czechoslovakia, and Germany, and eastward via the Bering Isthmus to the Yukon, Kansas and Texas. Sher (1971, p. 233) suggests that ..."*Soergelia* was very widespread in the Early Pleistocene and can serve as one of the characteristic 'guide' fossils for that stage". I think we can be more precise. In my opinion, the evidence is sufficiently strong to say that specimens of *Soergelia* are indicative of sediments of Kansan glacial age, and that *Soergelia* fossils are extremely valuable from a biostratigraphic viewpoint,

allowing Kansan deposits of Texas and Kansas in North America to be correlated with deposits of the Olyor Suite and its equivalents in the Soviet Union, and with Mindel and Elster sediments in Europe. Also, I infer that there are (or were) unrecognized fossiliferous sediments of Kansan age exposed within the Old Crow Basin of the Yukon Territory.

Soergelia probably looked like a cross between a tundra muskox (*Ovibos moschatus*) and a mountain sheep. A comparison of metapodials suggests that *Soergelia* was lighter and more slender-limbed than the tundra muskox, and that it had relatively long metatarsals. It seems to have preferred cool, tundra-like or cool, dry park-land habitat, and I think it is a paleoenvironmental indicator of those conditions. In northeastern Siberia it was able to live in tundra-like surroundings, with the addition of some steppe elements (Gitterman 1973, p. 67). The fact that it was associated with steppe mammoth (*Mammuthus armeniacus*), caribou (*Rangifer tarandus*) and giant moose (*Alces latifrons*) at Süssenborn in East Germany, suggests that *Soergelia* occupied cool steppe or tundra there. Faunal associates of *Soergelia* cf. *elisabethae* at Rock Creek, Texas were mammoths (*Mammuthus* sp.),

large ground sloths (*Paramylodon* sp.), camels (*Camelops* sp.), and horses (*Equus* sp.), which suggest cool, parkland conditions. Probably Soergel's muskox fed mainly on grasses and shrubs. Perhaps wolves, which are members of the Rock Creek, Olyor, and Süssenborn faunas, were among its main predators.

Bootherium sargenti (Sargent's muskox)

A single specimen of Sargent's muskox (Figure 83A-C, Table 96) has been collected from Pleistocene deposits in the Yukon Territory. Probably all specimens referable to this species represent females of *Symbos cavifrons*. Facts supporting this contention are provided below.

Referred specimen

NMC 10536 from Old Crow Locality 9 consists of the proximal half of a right horncore with a large part of the adjacent frontal region. The following features characterize this specimen and *Bootherium sargenti*: (a) a definite burr at the base of the horncore; (b) a horncore, somewhat dorsoventrally compressed near the base which projects laterally for about 75 mm in the frontal plane, then curves down and forward in a graceful arc; (c) a broad space across the frontals between horncore burrs. Through the courtesy of C.E. Ray of the

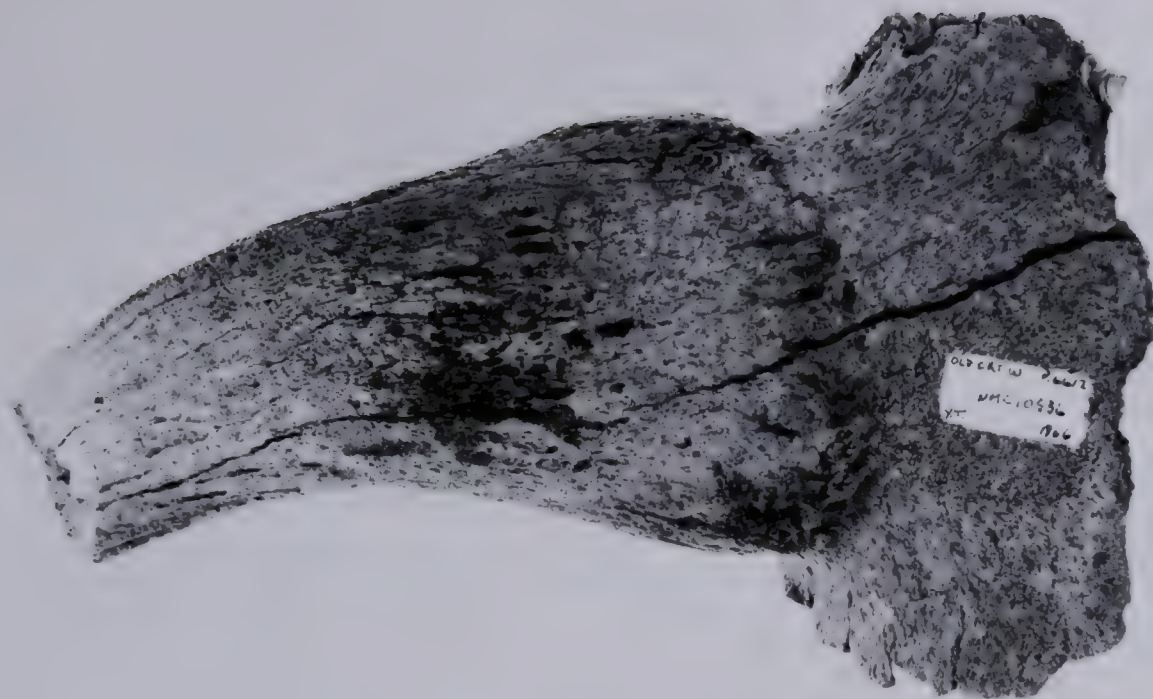
Figure 83. Right horncore lacking tip with attached cranial fragment (NMC 10536, Old Crow Locality 9) of a Pleistocene Sargent's muskox (*Boötherium sargenti*).

A. Dorsal view (anterior to bottom).

B. Anterior view.

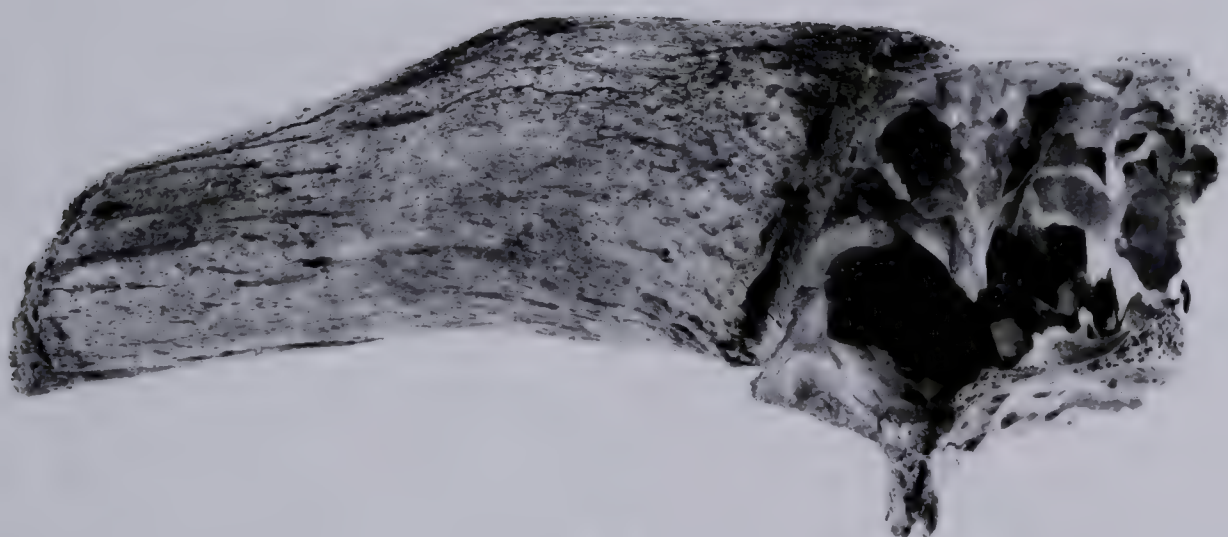
C. Ventral view (anterior to top).

Probably *Boötherium sargenti* is a female of the helmeted muskox *Symbos cavifrons*.



5 CM

A



B

5 CM



C

5 CM

Table 96. Measurements of a Pleistocene Sargent's muskox (*Bootherium sargenti*) horncore from the Yukon Territory compared to horncores of *Bootherium sargenti* (= *Bootherium nivicolens*) from Alaska.

Specimens	Measurements (mm)*			
	1	2	3	4
<i>Bootherium sargenti</i> . Pleistocene, Y.T.				
NMC 10536 Old Crow Loc. 9	81.0	64.2	230.0	52.0
<i>Bootherium sargenti</i> . Pleistocene, Michigan				
GRPM 11 423 3101 (type) Grand Rapids	80.0	68.0	242.0	-
<i>Bootherium sargenti</i> . Pleistocene, Alaska				
(= " <i>Bootherium nivicolens</i> " type) Eschscholtz Bay				
USNM 2324 Subadult?	63.0	58.0	200.0	46.0

* 1 - Transverse diameter of horncore at burr.

2 - Vertical diameter of horncore at burr.

3 - Circumference of horncore at burr.

4 - Thickness of braincase at frontal (between anterior horncore bases).

United States National Museum, I was able to compare the Yukon specimen with the types of *Boötherium sargenti* (GRPM 11 423 3101), "*Boötherium nivicolens*" (USNM 2324), and *Boötherium bombifrons* (ANSP 2994). In my opinion, NMC 10536 is not closely related to *Boötherium bombifrons*. Unlike the type specimen of the latter species, NMC 10536 has no pronounced pedicel, has less sharply dropping horncores, and is markedly larger. In shape and flare of the horncores NMC 10536 is close to "*Boötherium nivicolens*", but it is closest in size and general form to the type of *Boötherium sargenti* and is referred to that species. While comparing the specimens, I noticed that the type of "*Boötherium nivicolens*" from Alaska had unfused sutures, which, considering its smaller size, suggests that it may represent an animal that was not fully mature when it died. Because of this, and the fact that both it and the Yukon specimen are from Eastern Beringia, I consider "*Boötherium nivicolens*" to be a junior synonym of *Boötherium sargenti*.

Two other specimens from the Yukon Territory may pertain to *Boötherium sargenti*. NMC 17613 from Herschel Locality 1 is a right tibia, which is abraded on the lateral and posterior borders of the proximal articulation. Morphologically, it matches well a tibia of Recent *Ovibos moschatus*, but it is longer (total length 390 mm)

and more slender than that species (total length 376 mm (Cornwall 1964, p. 169)). The Herschel Island fossil appears to have the proportions and features of a tibia of *Symbos cavifrons* (total length 455 mm (Semken *et al.* 1964, p. 839)), but it is shorter. Therefore, NMC 17613 is tentatively referred to ?*Boötherium* sp. There seems to be no way of checking the identification at present, for no *Boötherium* or *Praeovibos* (which it could also represent) tibiae have been described.

Quackenbush (1909, p. 127) identified *Boötherium bombifrons* from "a very good photograph" (presumably of a skull fragment) taken by T. Obalski at Gold Run Creek (Dawson Locality 32) in July 1903. This photograph was in the possession of Henry Fairfield Osborn, but could not be located in his files (R.H. Tedford, personal communication 1972). Although Obalski (1904, p. 216) includes the muskox ("le Boeuf musqué") in a list of remains of Pleistocene mammalian species he had seen in the Yukon, he does not designate the species nor the exact locality where it was found. Species of *Boötherium* would be difficult to identify from a photograph alone, and because I have not been able to examine Obalski's photograph, I feel that the presence of *Boötherium* sp. in the Gold Run Creek fauna is questionable. The only

definite report of *Boötherium* in Canada is from the Old Crow Basin, Yukon Territory.

Discussion

In the conterminous United States, *Boötherium sargenti* has been described from Nebraska, Utah, Missouri, Indiana, Texas and Pennsylvania. The type specimen of this species consists of most of a cranium with horncores from a postglacial bog near Grand Rapids, Michigan. *Boötherium* sp. has been reported from Saltville, Virginia; Douglas County, Nebraska; and Neeley, Idaho (E. Anderson, personal communication 1976). The Saltville specimen is particularly interesting because of its large size relative to the type of *Boötherium sargenti* (Ray *et al.* 1967, Table 5). Probably most of these specimens are of Wisconsin age.

Although *Boötherium bombifrons* has been reported from places other than the type locality, Big Bone Lick, Kentucky (e.g. Frankstown Cave, Pennsylvania, where the only parts of the skull preserved are the basicranial region and dentition (Peterson 1926, pp. 260-261) - parts inadequate for specific identification in my opinion), I am aware of no other specimen like the type. Therefore, I consider that most records of *Boötherium* pertain to *Boötherium sargenti*. Presuming the specimen of *Boötherium bombifrons* does not represent an abnormal individual,

that species is probably not closely related to *Boötherium sargenti* or *Sumbos cavifrons*. In this respect, Allen (1913, p. 212) concluded: "*Boötherium* {*Boötherium bombifrons*} and *Preptoceras* { = *Euceratherium*} are not closely related, but more nearly so than is either to any other known genus."

A specimen referred to "*Boötherium* sp." was recovered from deposits of probable Illinoian age at Cripple Creek sump near Fairbanks, Alaska (Péwé and Hopkins 1967, pp. 268-269). It is the earliest record of the genus in North America. Several other cranial fragments of *Boötherium sargenti* (= *Boötherium nivicolens*) are known from that state. At least three have been collected from Pleistocene deposits in the Fairbanks area, and the type of "*Boötherium nivicolens*" is from Eschscholtz Bay on the west coast of Alaska. A nearly complete carcass of a small extinct muskox, possibly *Boötherium sargenti*, was preserved in muck on a creek near Fairbanks (Guthrie 1972, p. 300). Samples of hair and dessicated flesh from the specimen gave radiocarbon dates of $17,210 \pm 500$ years B.P. (SI-454) and $24,140 \pm 2,200$ years B.P. (SI-455), respectively. A hornsheath from *Boötherium sargenti* from Fairbanks Creek yielded a radiocarbon date of $22,540 \pm 900$ years B.P. (SI-292). These dates indicate that Sargent's muskox lived in Eastern Beringia during the peak of the Wisconsin glaciation.

Allen (1913, p. 215), Hibbard and Hinds (1960, p. 107), and Semken *et al.* (1964, p. 824) consider that *Boötherium sargenti* is a female of *Symbos cavifrons*. I think the evidence supporting this view is very strong. The similar basic conformation of the horncores (as far as orientation and curvature are concerned); the smaller, thinner-roofed cranium; and the broad space between the horncore bases in the former species parallel the differences between male and female *Ovibos moschatus*: thus Sargent's muskox resembles what a female *Symbos cavifrons* would be expected to look like. In addition, *Boötherium sargenti* and *Symbos cavifrons* had similar geographic and habitat preferences, for both are found in the same states or provinces (e.g. Alaska, Yukon Territory, Indiana, Michigan, Virginia (using *Boötherium* sp.), Utah, Missouri and Nebraska), and sometimes even from the same site and deposit (e.g. near Great Salt Lake, Utah, in the Bonneville sands and gravels (Stokes and Hansen 1937, p. 63), and evidently in the Goldstream Formation of Wisconsin age near Fairbanks, Alaska). In the conterminous United States, both species are concentrated within the same latitudinal range — usually south of the late Wisconsin fossil localities of the tundra muskox, *Ovibos moschatus*. Unlike

Soergelia, *Praeovibos*, and *Ovibos*, which had Holarctic distributions during the Pleistocene, *Boötherium sargenti* and *Symbos cavifrons* are only known from North America. Geochronologically, both species appear during the Illinoian and become extinct near the close of the Wisconsin glaciation.

I estimate that *Boötherium sargenti* was about 25% smaller than *Symbos cavifrons*. Like *Symbos*, it probably had dark brown fur, and possibly a shorter coat than *Ovibos* (Harrington 1968, p. 1162). The horns branched laterally, then curved downward and forward. They did not meet at the bases. A colored illustration of a group of Sargent's muskoxen is provided in a wall chart accompanying an article by Guthrie (1972). Probably these animals were primarily grazers and secondarily browsers, preferring cool steppe grasslands or parklands. Perhaps wolves were their main predators.

Symbos cavifrons (helmeted muskox)

Symbos remains are not uncommon in collections from Yukon Pleistocene deposits, but they are much rarer than bison fossils. Several cranial fragments (one from Alaska), three mandibular fragments and a metatarsal are described (Figures 84A-C, 85A-C, 86A-C, 87, Tables 97-99). A relatively small cranial specimen (USNM 2555) from Lovett Gulch on Bonanza Creek near Dawson was described as the type of a new species, *Symbos tyrrelli* (= "*Scaphoceros tyrrelli*"; Osgood 1905a, p. 174). Larger crania of adult males have been found at two localities within a mile (1.6 km) of the place where the type specimen of *Symbos tyrrelli* was collected. Evidently USNM 2555 lies within the lower range of measurements for adult crania of *Symbos cavifrons* (Table 97). It differs in no qualitative way from *Symbos cavifrons*, and I (Harington 1968, pp. 1163-1164) consider *Symbos tyrrelli* to be a junior synonym of *Symbos cavifrons*. The probability that *Symbos cavifrons* is a male and *Bootherium sargenti* is a female of the same species has been discussed under the latter heading.

Referred specimens

NMC 29229 from Dawson Locality 1 is the posterior half of a large cranium lacking the distal third of the left horncore, and the distal two-thirds of the right horncore. The upper parts of the orbits are present, but are

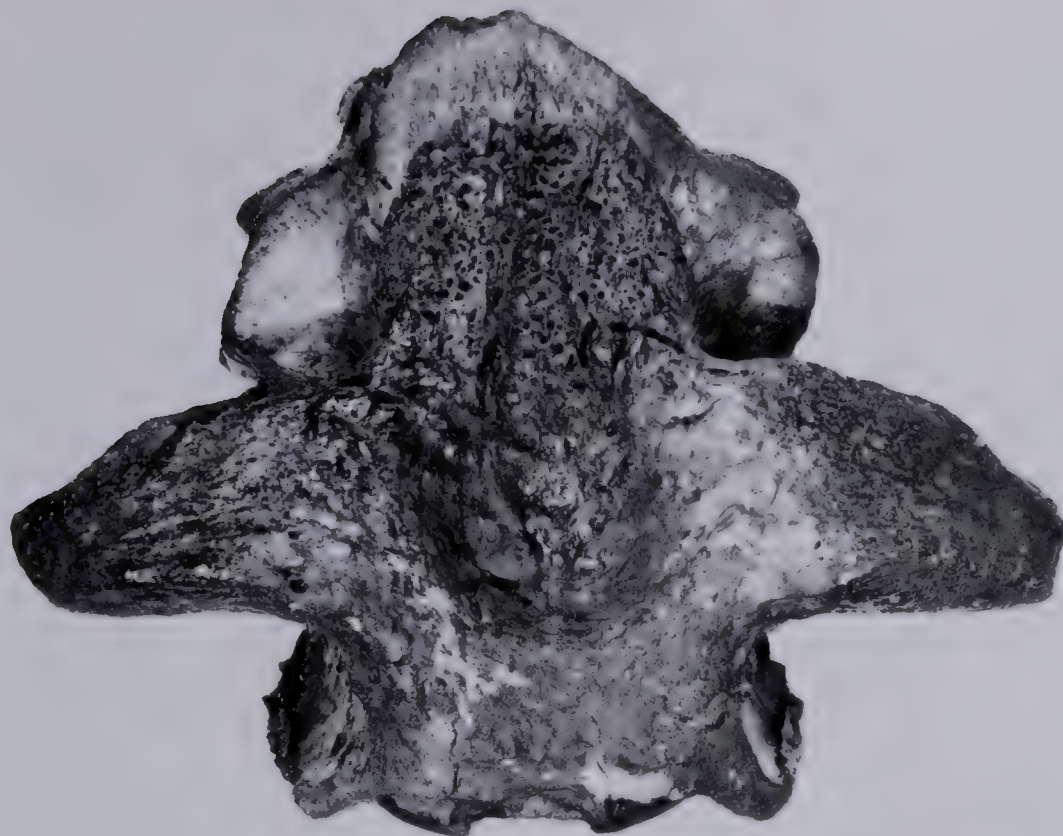
Figure 84. Posterior of cranium with complete
horncores (NMC 8837, Dawson Area - locality
unknown) of a Pleistocene helmeted muskox
(*Symbos cavifrons*).

A. Dorsal view (anterior to top).

B. Posterior view.

C. Ventral view (anterior to bottom).

Original pale colored bone is largely
covered by dark brown shellac.



A



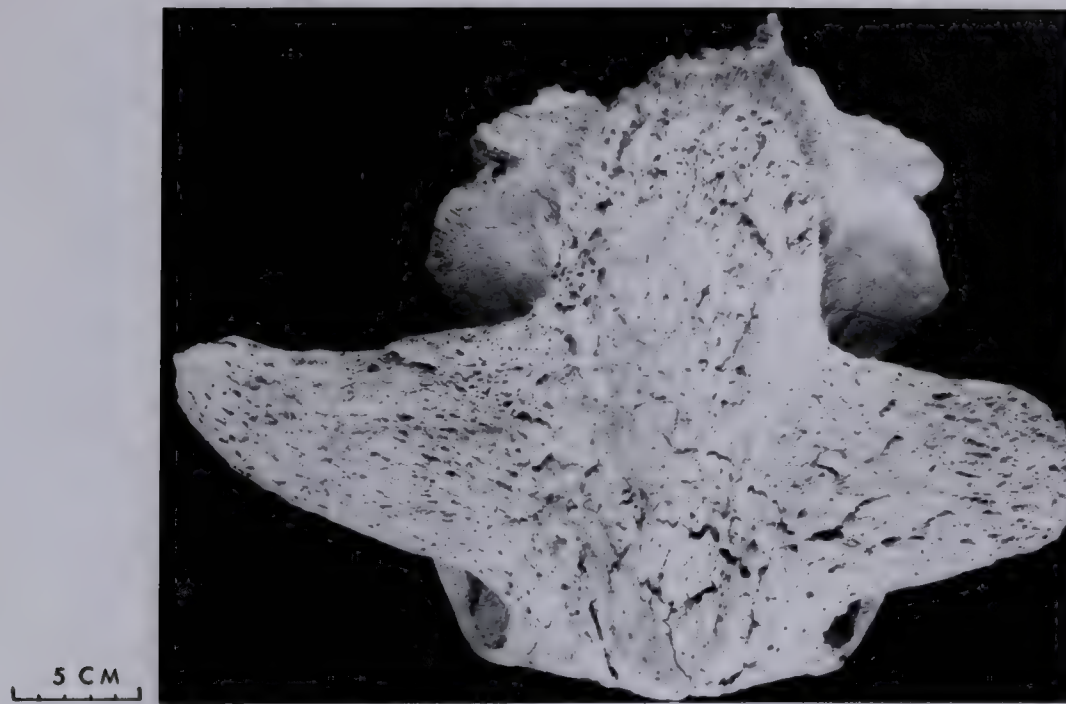
B



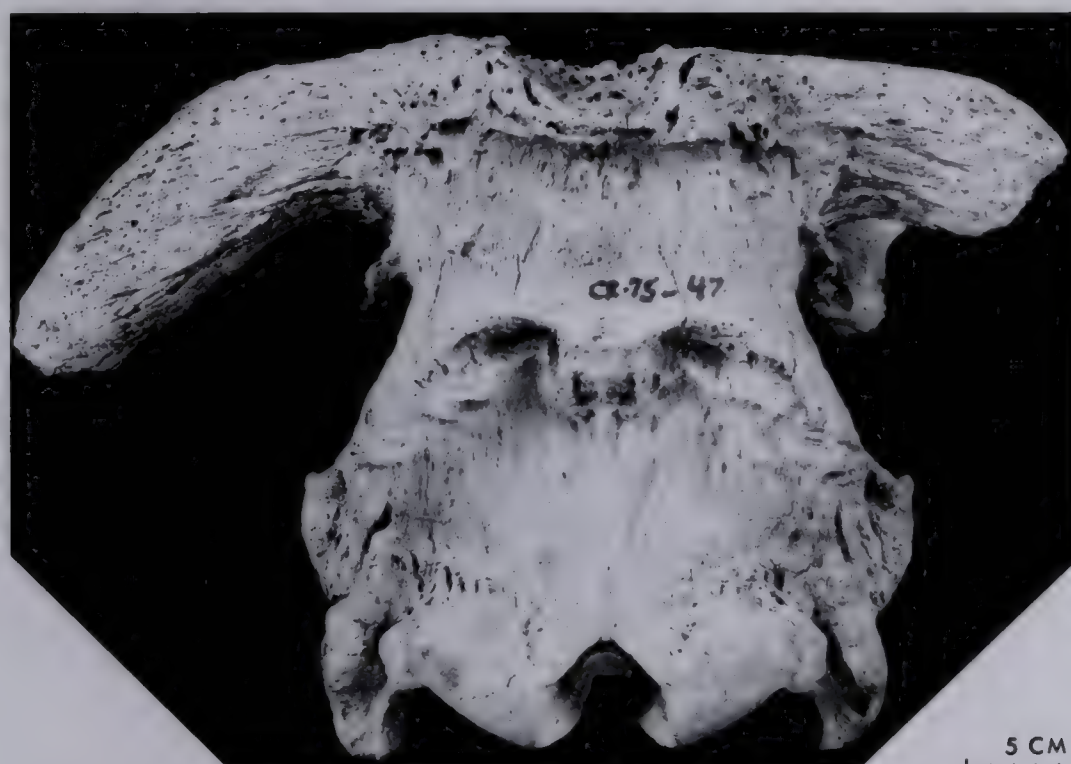
C



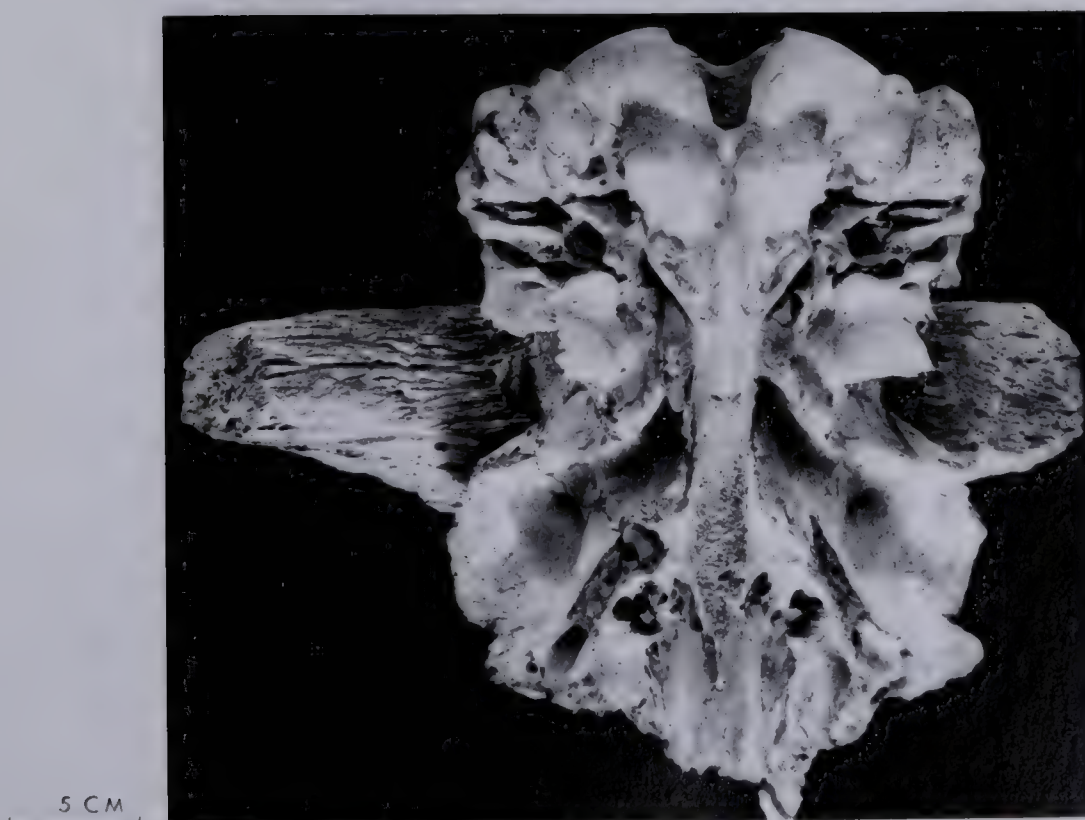
Figure 85. Posterior of cranium with partial horn-
cores (NMC 29229, Dawson Locality 1) of a
Pleistocene helmeted muskox (*Symbolos cavifrons*).
A. Dorsal view (anterior to top).
B. Posterior view.
C. Ventral view (anterior to bottom).



A



B



C



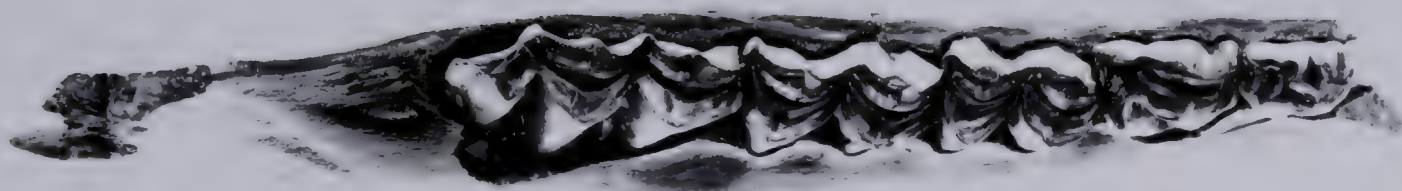
Figure 86. Right mandibular fragment with RP_3 - RM_3
(NMC 14170, Old Crow Locality 11) of a
Pleistocene helmeted muskox (*Symbos*
cavifrons).

- A. Lateral view.
- B. Occlusal view.
- C. Medial view.

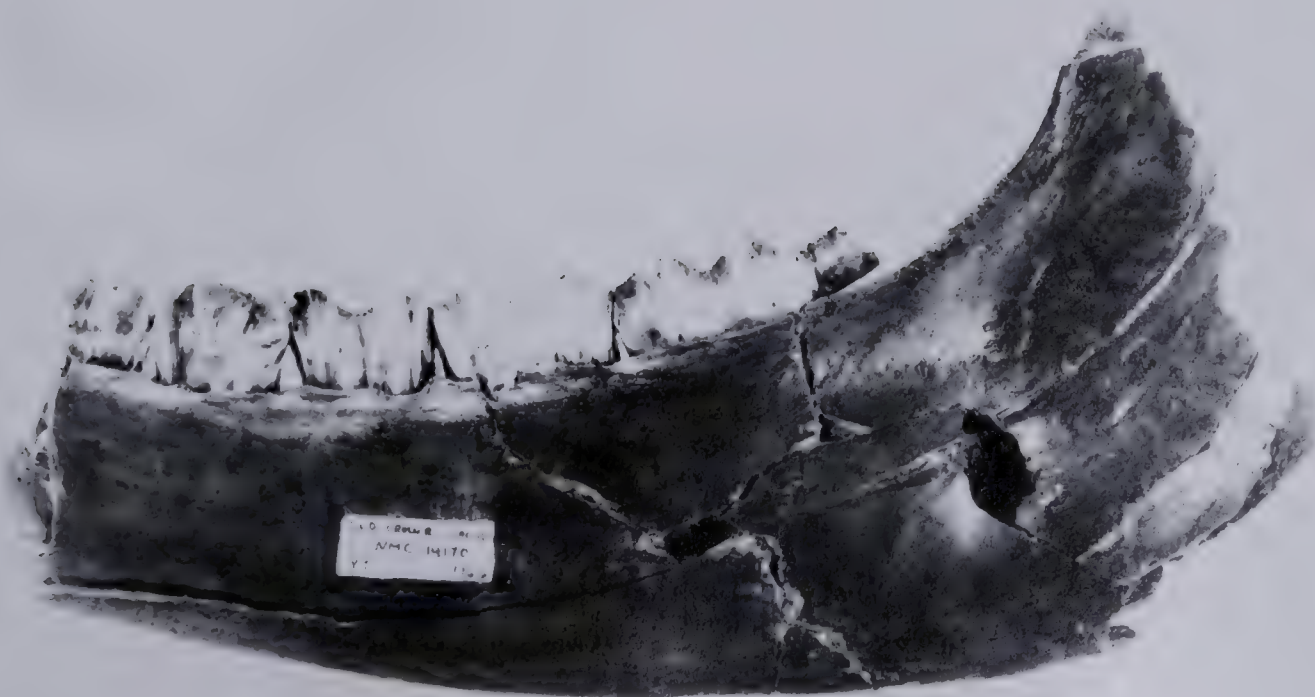


A

5 CM



B



C

5 CM



Figure 87. Restoration of a helmeted muskox (*Symbos
cavifrons*) tossing a wolf (*Canis lupus*).
Ink sketch by Bonnie Dalzell.



Table 97. Measurements of Pleistocene helmeted muskox (*Symbos cavifrons*) crania from the Yukon Territory compared to *Symbos cavifrons* crania from Alaska and Alberta.

Specimens	Measurements (mm)*																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
<i>Symbos cavifrons</i> .																		
Pleistocene, Y.T.																		
NMC 29229 Dawson Loc. 1	241.1	117.7	109.8a	59.0	-	-	132.0	-	123.2	165.0	192.1	102.9	41.0	42.4	145.4	57.2	202.0	75.9
NMC 8837 Dawson Area	230.3	117.1	99.4	55.7	195.0	280.0	124.0	421.5	133.9	130.5 [†]	162.5 [†]	110.5	43.0	47.9	150.4	52.3	208.0	87.3
USNM 2555 (type of " <i>Symbos tyrelli</i> ") (Osgood 1905, p. 184) Lovett Gulch - adjoins Dawson Loc. 1	214.0	114.0	95.0	72.0	-	-	-	-	117.0	-	-	-	-	-	-	-	197.0	72.0
NMC 11370 Dawson Loc. 2	237.5 [†]	110.0a	115.6	71.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-
DCMP 10 Dawson Area	-	-	115.0a	-	227.0	287.0	-	-	-	-	-	-	-	-	-	-	-	-
NMC 26920 Old Crow Loc. 21	-	103.0 [†]	86.7 [†]	66.7	-	-	-	-	110.0	-	-	-	-	-	-	-	-	-
<i>Symbos cavifrons</i> .																		
Pleistocene, Alaska																		
NMC 25892 Lost Chicken Ck.	232.9	117.1	110.4	77.6	234.0	305.0	145.0	522.0e	124.3	129.1	172.6	95.5e	45.1	46.8	142.0	52.7	212.5 [†]	78.9
<i>Symbos cavifrons</i> .																		
Pleistocene, Alberta (Harrington 1975c, Table 2)																		
Unencataloged Fox Saskatchewan	240.5	124.5	114.5	54.5	-	-	142.1	500.0 [†] e	117.5	146.5	191.0	101.2	42.0	49.8	152.9	58.4	201.9 [†]	84.4

- *1 - Exostosis length.
 2 - Exostosis width anterior to horncores.
 3 - Anteroposterior diameter of horncore at base (where narrowing begins).
 4 -orsoventral diameter of horncore at base.
 5 - Length of horncore on lower curve (ridge to tip).
 6 - Length of horncore on upper curve (edge of depression to tip).
 7 - Width of cranium at constriction between horncores and orbits.
 8 - Minimum width between horncore tips.
 9 - Width of cranium at constriction above nuchal crest.
 10 - Height from dorsal margin of foramen magnum to mid-line on dorsal surface of cranium.
 11 - Height from ventral margin of foramen magnum to top of nuchal crest.
 12 - Height from dorsal margin of foramen magnum to top of nuchal crest.
 13 - Height of foramen magnum.
 14 - Width of foramen magnum.
 15 - Width across occipital condyles.
 16 - Width of right occipital condyle.
 17 - Maximum width of cranium above auditory meatus.
 18 - Basioccipital width (across posterolateral margins).

heavily eroded. Bone is missing anterior to the forward ridge of the exostosis (the roughened central region of the cranium between the horncores). The surface is pale and slightly iron-stained. NMC 8837 was collected from an unknown locality in the Dawson Area about 1916. It consists of the posterior half of a cranium with complete horncores: the right one is slightly longer than the left. The fossil is like NMC 29229 except that bone above the nuchal crest is much thinner (disregarding some erosion that has occurred at this point), and the region between the horncore bases is deeply excavated and bowl-shaped. However, I have noticed that the thickness of bone above the nuchal crest varies greatly in the extant muskox, *Ovibos moschatus*, and I do not regard it as of taxonomic importance. The rough, trough-like areas between the horncores of *Symbos* are also irregular in form. The surface of NMC 8837 is covered with brown commercial preservative, but the underlying bone is fresh-looking.

USNM 2555 from Lovett Gulch near Dawson is the type of "*Symbos tyrrelli*". It is a relatively small, well preserved cranium with some parts missing from one side. LP_2-LM_3 and RM_2-RM_3 are intact. Evidently the cranium represents a very old individual, for the teeth are heavily worn. The bone is brownish in color, but is not heavily permineralized (Osgood 1905, p. 173). It is worth noting that this specimen was collected within half

a mile (0.8 km) of the large cranial fragment from Trail Creek (NMC 29229, Dawson Locality 1). USNM 2555 and another fossil (USNM catalog number unknown), comprising the posterior part of a cranium with an attached horncore, were presented to W.H. Osgood by J.B. Tyrrell, the Canadian geologist and explorer, in 1904.

NMC 11370 from Dawson Locality 2 (within a mile (1.6 km) of the site where "*Symbos tyrrelli*" was found) is a heavily eroded upper portion of a posterior cranial fragment. The trough-like region between the horncore bases is preserved. The bone is dark brown, with buff mottling on the dorsal surface. NMC 26920 from Old Crow Locality 21 is the upper part of a posterior cranial fragment with stubs of the horncores. It has the basic characteristics of *Symbos*, but it is smaller than the other specimens. Heavy erosion has worn away most of the rough exostoseal bone in the central trough exposing the frontals and revealing that the frontal suture is open. Therefore, I consider it to represent a subadult male, and tentatively, refer it to *Symbos cavifrons*. The bone is stained dark, rusty brown, and may be of pre- late Wisconsin age. DCMP 10 from the Dawson Area is a virtually complete horncore. It is displayed in the Dawson City Museum.

Three mandibular fragments are in the Yukon collections. NMC 14170 from Old Crow Locality 12 is the central part of a right mandible with RP_3 - RM_3 . RP_2 , bone anterior to RP_3 , and the ascending ramus are lacking. The specimen probably represents an animal in early maturity, for RM_3 has not fully erupted, nor is the posterior-most cusp completely worn. It is somewhat smaller than the mandible of a large adult of *Symbos cavifrons* (= "*Ovibos giganteus*" - F:AM Field No. $\frac{4254}{1939}$) from near Fairbanks, Alaska to which it was compared. NMC 14170 has several interesting features. An unworn labial style is situated between the crescents of RM_1 . RP_3 is highly developed in *Symbos* compared to *Ovibos moschatus* - possibly representing the more primitive condition in muskoxen. In the course of eruption and wear, an anterior chip of RM_1 was dislodged and preserved in a depression in the posterior lobe of RP_4 . The surface of the chip was worn nearly flush with the occlusal surface of RM_1 . The bone is dark brown, as is the dentine, suggesting a pre- late Wisconsin age. I am grateful to C.E. Ray for allowing me to compare this fossil with F:AM Field No. $\frac{4254}{1939}$, which was temporarily in his custody, and to M.F. Skinner for assisting me with the comparison.

NMC 25171 from Dawson Locality 16 is a right mandible lacking the ascending ramus, the anterior tip of the horizontal

ramus, RP_2 , and most of RP_3 and RP_4 above the roots. A symphyseal portion of the left mandible is attached. Occlusal wear on RM_1 - RM_3 suggests that the animal represented was mature. The loops of RM_1 are greatly reduced. The bone is pale tan, and the enamel is rather fresh-looking. The specimen may be of late Wisconsin age. A more deeply stained diastema region of a right mandible, NMC 28547 from Old Crow Locality 144, compares well with that part of NMC 25171, and is referred to *Symbos cavifrons*. It is interesting to note that the diastema of *Symbos cavifrons* is unusually long: that of NMC 25171 (154.3 mm) is slightly longer than the diastema of a Recent moose (*Alces alces*, NMC 4412) from New Brunswick (152.2 mm). Did similar feeding habits result in this parallelism? In any case, the helmeted muskox had a relatively long snout compared to the living tundra muskox. Both NMC 28547 and 25171 have two large mental foramina (the lower one just anterior to the upper) which are situated in the upper half of the mandible approximately 100 mm in front of the anterior alveolar margin of RP_2 . A keel is developed on the dorsal surface of the diastema regions of both NMC 28547 and 25171.

NMC 14495 from Old Crow Locality 22 is a complete right metatarsal. It is too long and slender to be a metatarsal of any other muskox known from Yukon Pleistocene

deposits (e.g. *Soergelia*, *Praeovibos*, *Ovibos*), yet it matches well in all morphological features a metatarsal of *Ovibos moschatus* (NMC 29185). NMC 14495 with a total length of 227.7 mm is approximately 11% longer than *Praeovibos* sp. metatarsals from Siberia and approximately 30% longer than *Ovibos moschatus* (Table 100), and is referred to *Symbos cavifrons*. The fossil is stained dark brown and is probably pre- late Wisconsin in age.

Discussion

The helmeted muskox is known from both Dawson and Old Crow areas in the Yukon Territory. The degree of staining of the specimens suggests that most are of late Wisconsin age, and that a few are of pre- late Wisconsin age.

In other parts of Canada, *Symbos cavifrons* has been reported from British Columbia, Alberta and Saskatchewan. A well preserved cranium (NMC 11859, displayed in the National Museum of Natural Sciences, Ottawa) and two cranial fragments (SMNH 1280/4321, 1164/7750) have been collected from deposits probably of Sangamon interglacial age at Fort Qu'Appelle, Saskatchewan (Harrington 1961, p. 460; Khan 1970, pp. 64-75). A posterior cranial fragment (UA* uncataloged) of this species was collected at Fort Saskatchewan, Alberta from a gravel and sand unit overlying grayish-blue bentonitic sandstone of the

Edmonton Formation (Cretaceous). It was overlain by a unit of postglacial silt and sand. The fossil was deposited following the initial glaciation of the region by Keewatin ice. Probably the specimen is of late Pleistocene age (Harington 1975c, p. 906). A heavily eroded posterior cranial fragment (BCPM 680) of *Symbos* sp. from near Dease Lake, British Columbia probably dates to a non-glacial phase of the Pleistocene. Tough, gray mudstone adhering to protected areas of the cranium may indicate a relatively great age for this specimen (Harington 1968, p. 1164). A cranial fragment (BCPM 69: 014) from gravels on the Saanich Peninsula of Vancouver Island indicates that helmeted muskoxen reached the island via a land connection during the Olympia Interglaciation, or possibly during glacial maxima of the late Pleistocene, when land may have been exposed between the mainland and Vancouver Island (Harington 1975c, pp. 911-915).

In the conterminous United States a total of 40 or more specimens are known from the following states: Arkansas, California, Colorado, Idaho, Illinois, Indiana, Iowa, Kansas, Kentucky, Michigan, Missouri, Nebraska, New Mexico, North Dakota, Ohio, Oklahoma, Utah, Virginia, Washington (C.E. Ray, personal communication 1968), Wisconsin, and the continental shelf 40 miles (64.4 km) southeast of Atlantic City, New Jersey (D. Baird, personal communication 1961). Specimens from Mullen II on the

Middle Loup River, Nebraska (Jakway 1961, pp. 114-115) and from Conard Fissure, Arkansas indicate that *Symbos cavifrons* had reached western and south-central United States by early Illinoian time. Probably most specimens from the conterminous United States are of Wisconsin age. Bone of *Symbos cavifrons* from a marl deposit in Kalamazoo County, Michigan yielded a radiocarbon date of $13,200 \pm 600$ years B.P. (M-639) (Hibbard and Hinds 1960, p. 105). A radiocarbon date pertaining to a muskox from Scotts, also in Kalamazoo County, Michigan, is $11,100 \pm 400$ years B.P. (Semken *et al.* 1964, p. 833). Apparently the latter date is near the time of extinction of *Symbos cavifrons* in the southern refugium.

Perhaps 20 or more specimens of *Symbos cavifrons* are known from Alaska. Most are from the Fairbanks region and are preserved in the Frick Collection of the American Museum of Natural History in New York. Other specimens have been reported from Anvik in the west (Osgood 1905a, p. 183), near Point Barrow on the northern coast (Harington 1968, p. 1164) and from Lost Chicken Creek in the east. The specimen (NMC 25892) from the last locality is very fresh-looking, and is probably of late Wisconsin age. It is a posterior cranial fragment with a complete left horncore and a third of the right horncore. The fossil lacks bone anterior to the orbits, which are partly preserved. The occipital region is eroded, particularly

on the lateral margins and on the upper parts of the occipital condyles. Surface details of the rugose, central channel, and horncores are well preserved. The thickness of bone above the nuchal crest in NMC 25892 is intermediate between the great mass in NMC 29229 from Dawson Locality 1 and NMC 8837 from the Dawson Area, in which little bone is present above the nuchal crest. A *Symbos* specimen from deposits considered to be of Illinoian age at Cripple Creek sump near Fairbanks (Péwé 1975a, Table 11) is the earliest known from Eastern Beringia. Winter fecal pellets associated with hair and a skeleton of *Symbos cavifrons* from Little Eldorado Creek gave a date of >40,000 years B.P. (SI-291). Radiocarbon analyses of horns sheaths from two specimens of the helmeted muskox from near Fairbanks (Dome Creek and Upper Cleary Creek) yielded dates of $17,695 \pm 445$ years B.P. (SI-851) and $25,090 \pm 1,070$ years B.P. (SI-850), indicating that *Symbos* occupied Eastern Beringia during the peak of the Wisconsin glaciation.

Symbos cavifrons has not been reported from Eurasia. However, I suspect that the heavily eroded type specimen of *Ovibos recticornis* (Ryziewicz 1933, Plate 5-1a, b) is closely related to the genus *Symbos*, being like it in the following characteristics: (a) great depth from

the lower lip of the foramen magnum to the dorsal surface of the cranium between the horncores: *Praeovibos* and *Ovibos* are shallower and broader in the occipital region; (b) the marked constriction of the occipital region near the level of the nuchal crest, unlike that of most *Praeovibos* and *Ovibos* skulls; (c) ridges near the bases of the horncores, bordering the area where the central channel or trough occurs in *Symbos*, and unlike the situation in *Praeovibos* in which the horncore bases tend to be narrower anteroposteriorly and encroach more on the frontals, or the situation in *Ovibos* in which horncore bases nearly meet at the frontal suture, leaving a narrow anteroposterior groove there; and (d) horncores departing from the cranium nearly level with the frontal plane before being deflected down, and therefore flaring more than the horncores of *Praeovibos* or *Ovibos*. It is interesting to note that in comparing the type specimen of *Ovibos recticornis* with crania of other fossil muskoxen, Ryziewicz (1933, p. 85) commented that it could be closer to the type specimen of "*Gidleya zuniensis*" (a heavily-worn *Symbos cavifrons* cranial fragment according to C.E. Ray, personal communication 1968) than to specimens of *Ovibos fossilis*. Evidently any rough bone that may have existed in the trough between the horncores of the type of *Ovibos recticornis* has been eroded. Apparently this specimen is from Mindel (?Kansan) deposits at Radotin, Czechoslovakia. Perhaps Kretzoi (1942)

was correct in applying a new generic name "*Parovibos*" to this specimen, that is, if it does not belong to *Symbos*. In an effort to find out how well crania of *Ovibos recticornis* and *Symbos cavifrons* match, I have requested a cast of the type specimen of the former species.

Virtually nothing is known about the origins of *Symbos*. It undoubtedly had Eurasian ancestors, but the genus has not been reported definitely from that continent. I speculate that *Ovibos* and *Symbos* arose from the same basic, alpine-adapted ancestors; but *Symbos* has a few features that I regard as "less advanced" (e.g. higher set horns). Perhaps helmeted muskoxen evolved in broad intermontane valleys, dispersing onto the lower plains during the severe Illinoian glaciation as cool, steppe grasslands encroached on those areas, whence the animals spread through Alaska (Cripple Creek sump) and the Yukon to the south-central United States (Conard Fissure). Probably herds moved northward (Fort Qu'Appelle) as continental ice retreated during the Sangamon interglacial. *Symbos cavifrons* seems to have occurred in large numbers from the Pacific coast (e.g. California, Washington, British Columbia) to the Atlantic coast (e.g. continental shelf off New Jersey; Virginia) during the Wisconsin glaciation. Apparently

the species was widespread in unglaciated parts of Alaska and the Yukon then, dying out toward the close of the last glaciation. The most recent radiocarbon date for *Symbos cavifrons* from Alaska is approximately 17,700 years B.P. (Table 6), whereas the latest date of its occurrence in the southern refugium is approximately 11,000 years B.P.

Symbos cavifrons was taller and had a more slender build than the living muskox *Ovibos moschatus*. Its longer, deeper skull supported higher, more flaring horns with massive, fused bases (Figure 87). Hair found with a well preserved skeleton from Alaska (F:AM Field No. $\frac{4254}{1939}$) indicates that *Symbos* had a dark brown coat like *Ovibos*, but from the sample I examined, its hair seems to have been shorter and finer. Another indication that *Symbos* had a thinner coat than *Ovibos* and was adapted to warmer habitat is its relatively slight degree of orbital protrusion (these observations should be quantified). Parry (1821, Appendix P) among others, thought that the projection of the orbits in *Ovibos* served the purpose of carrying the eye clear of the hairy coat. Guthrie (1966, p. 725) has given evidence supporting the contention that cold-adapted, northerly ranging forms of *Bison* have more protruding orbits than southerly ones; the hypothesis being that peripheral

vision is facilitated in species requiring thick, cold-protective facial hair, by projection of the eye outward in a tubular socket. Perhaps for the same reason, orbits are prominent in tundra caribou, but not in woodland caribou, which are adapted to warmer environmental conditions (Banfield 1961, pp. 43, 70).

Little is known about the ecological requirements of *Symbos cavifrons*, but the distribution of their remains in southern North America (Kitts 1953; Harington 1961, Figure 25) shows clearly that these muskoxen were adapted to warmer (more southerly) conditions than *Ovibos*. In fact, *Symbos* was mainly confined to a belt across the central United States between 35°N and 43°N.

Hibbard (1951) considered that *Symbos cavifrons* was a woodland form, and concluded that the species foraged along lake and forest margins with woodland caribou in Michigan during the late Wisconsin. Kitts (1953) thought it possible that *Symbos* was a woodland or steppe form. Dillon (1956) suggested that *Symbos* and *Bootherium* were prairie rather than tundra animals because of the abundance of their remains throughout the grass belt of middle North America as far south as Texas. Benninghoff and Hibbard (1961), and Semken *et al.* (1964) reaffirmed

the woodland habitat of the helmeted muskox using fossil pollen as evidence. Yet it is interesting to note the approximate coincidence of *Symbos* range with former loess-steppe areas in the central United States (Flint 1971, Figure 9-14) and Alaska (Péwé 1975a, Figure 17). It is also worth noting that during the late Wisconsin, when *Symbos cavifrons* is known to have occupied the Fairbanks area, analyses of plant and invertebrate macrofossils in a 27 m core from sediments of that period indicate that forests "disappeared from interior Alaska or were greatly diminished and much of the region was characterized by steppe-tundra vegetation" (Matthews 1974, p. 828). Matthews adds that steppe conditions may have been favored by rapid deposition of primary and reworked loess.

The nature of the evidence concerning the habitat of this species is equivocal. Because there is still room for doubt that *Symbos* was a "woodland muskox", I suggest the use of a more descriptive, environmentally noncommittal name "helmeted muskox". Analysis of fecal remains associated with a skeleton of *Symbos cavifrons* from Alaska suggests that the individual represented by the bones had fed on grasses and sedges during the winter (Harrington 1968, p. 1165). Probably wolves were among its main predators.

Praeovibos priscus (Staudinger's muskox)

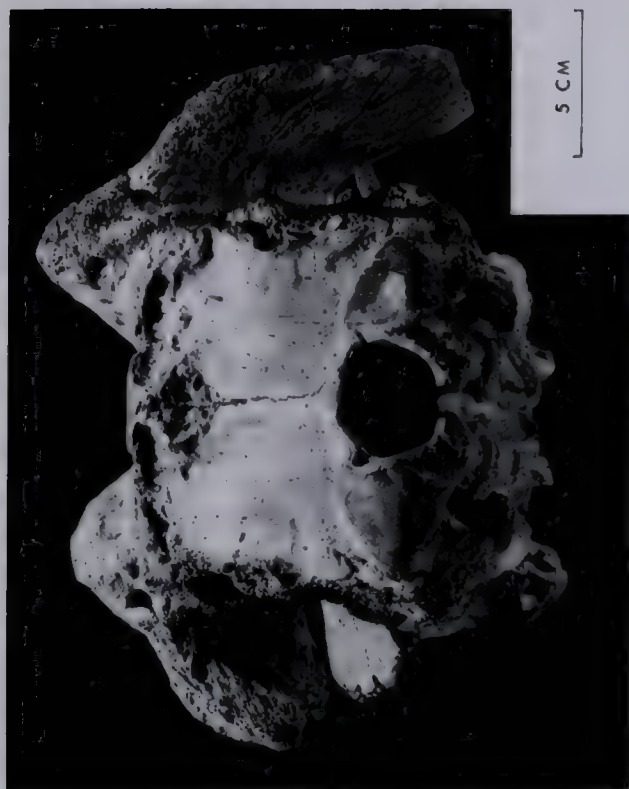
Twelve cranial fragments and two metapodials of Staudinger's muskox (Figures 88A-D, 89A-C, Tables 100-101) from Yukon Pleistocene deposits are described. They are the first records of this genus from the Yukon and Canada, and mark the easternmost limit of the species in North America. Historically, it is interesting that one of the first Pleistocene vertebrate fossils collected from the Yukon Territory was a partial cranium of *Praeovibos priscus*. Unfortunately it was identified as a specimen of the tundra muskox *Ovibos moschatus*, and its significance was overlooked (Lydekker 1885, p. 39). *Praeovibos* may be valuable as an index fossil of Illinoian age in Eastern Beringia. There is no evidence that it penetrated to southern North America.

Referred specimens

BM(NH) M 44070 is a posterior cranial fragment. Bone is lacking anterior to the orbits. Approximately two-thirds (150 mm) of the right horncore and half of the left horncore are preserved. Although the horncores are heavily eroded, their massiveness suggests that a male in early adulthood is represented. Only the upper portions of the orbits are preserved. The lateral margins of the occipital region are eroded. The frontoparietal and parietosquamosal sutures are not fused. The label on the



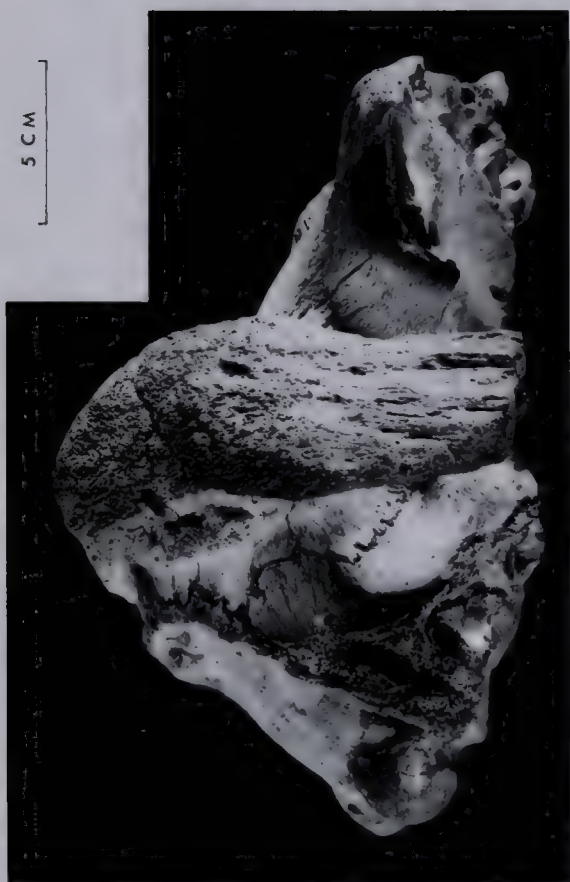
Figure 88. Posterior of cranium with partial horn-
cores (BM(NH) M 44070, Porcupine River -
locality unknown) of a Pleistocene
Staudinger's muskox (*Praeovibos priscus*).
A. Posterior view. B. Dorsal view.
C. Right lateral view. D. Ventral view.



A



B



C

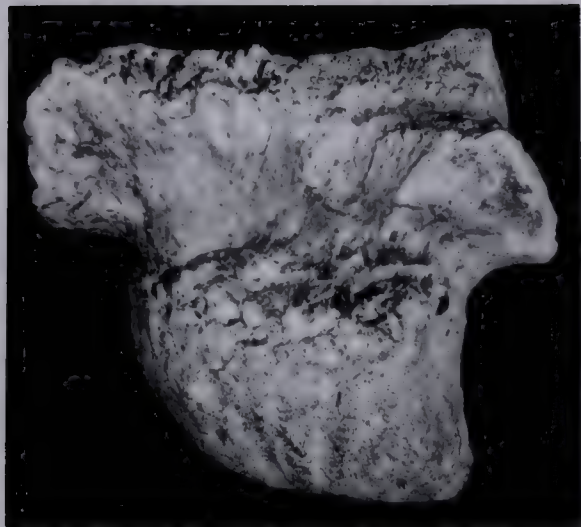


D

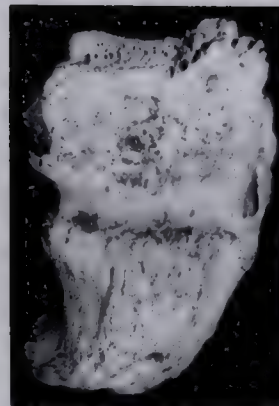


Figure 89. Partial left horncore with attached cranial fragment (NMC 20135, Old Crow Locality 74) of a male Pleistocene Staudinger's muskox (*Praeovibos priscus*) (left) and a partial right horncore with attached cranial fragment (NMC 20540, Old Crow Locality 22) of a ?female Pleistocene Staudinger's muskox (*Praeovibos priscus*) (right).

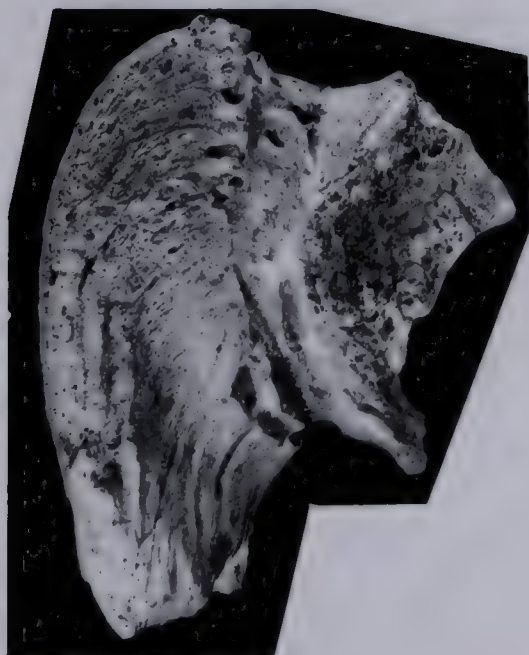
- A. Dorsal view.
- B. Lateral view.
- C. Posterior view.

**A**

5 CM

**B**

5 CM

**C**

5 CM

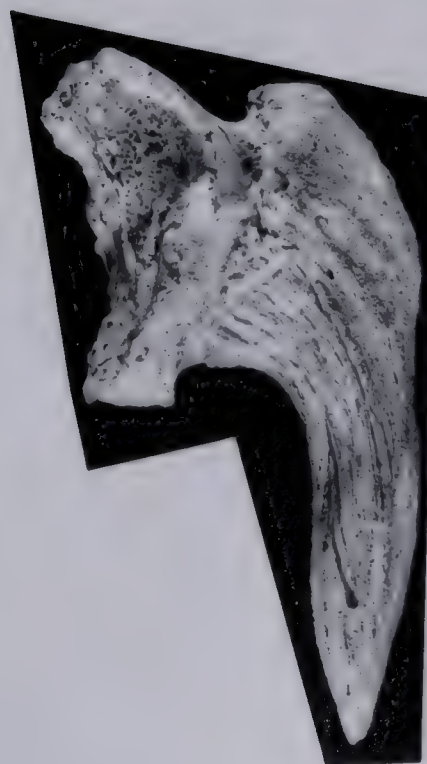


Table 100. Measurements of Pleistocene Staudinger's muskox (*Præovibos priscus*) crania and horncores from the Yukon Territory compared to those of *Præovibos priscus* from Siberia and Germany.

MEASUREMENTS (mm) *

SPECIMENS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
<i>Præovibos priscus</i> . Pleistocene, Y.T.																				
MALES (referred)																				
BM(NH) M 44070 Upper Porcupine R.		76.0	96.1	31.0 ⁺	57.5 ⁺	26.2	-	-	-	203.7 ⁺	97.1	45.4	103.3	98.0a	97.5	76.9	28.5a	32.4a	102.8	54.0
NMC 28100 Old Crow Loc. 109		-	-	-	-	-	-	-	-	-	-	-	-	-	105.4	84.1	27.4	33.3	109.5	61.0
NMC 20135 Old Crow Loc. 74		79.5	111.8	47.0	70.5	40.0	22.8	-	-	-	-	-	-	-	-	-	-	-	-	-
NMC 20607 Old Crow Loc. 20		77.7a	96.4	29.0	62.7	35.9a	16.0	-	-	-	-	-	-	-	-	-	-	-	-	-
NMC 27215 Old Crow Loc. 29		81.6	94.6	27.0	73.0a	35.0a	15.8	-	-	-	-	-	-	-	-	-	-	-	-	-
NMC 23057 Old Crow Loc. 11A		-	-	35.0 ⁺	72.4	41.6e	24.7	-	-	-	-	-	-	-	-	-	-	-	-	-
FEMALES (tentatively referred)																				
NMC 20540 Old Crow Loc. 22		54.3	67.4	18.5	38.1	21.6	18.0	99.0	169.0	-	-	-	-	-	-	-	-	-	-	-
NMC 15271 Old Crow Loc. 22		59.0	61.1 ⁺	18.0 ⁺	42.3	29.7	19.5a	78.0	151.0	-	-	-	-	-	-	-	-	-	-	-
NMC 27749 Old Crow Loc. 66		50.5a	74.3	19.0	41.8	27.1	13.3	-	-	-	-	-	-	-	-	-	-	-	-	-
NMC 19007 Old Crow Loc. 66		43.2	49.5	10.5	29.6	23.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Præovibos priscus</i> . Pleistocene, Siberia**																				
MALES																				
"OCX-73-761" exact locality unknown (very large cranium)		140.0 ⁺	-	-	-	-	-	300.0a	269.2e	121.3	48.2	120.4	-	118.7	89.8	-	-	130.6	72.8	
GIN $\frac{741-1}{109}$ Kolyma R.		83.7	-	-	-	-	-	153.0	257.0	-	95.2	46.7	96.0	-	104.8	82.2	-	-	109.8	55.8
FEMALES (referred by A.V. Sher)																				
GIN $\frac{851-72}{8}$ Krestovka R.		51.0	-	-	-	-	-	163.0	-	98.0	50.5	78.7	-	-	-	-	-	-	-	
"3100-920" exact locality unknown		61.3	-	-	-	-	-	-	-	98.0	49.0	88.2	-	-	-	-	-	-	-	
<i>Præovibos priscus</i> . Pleistocene, Germany																				
MALE (Sher 1971, Table 31) Catalog number unknown - Bad Frankenhausen (type)																				
		100.0	-	-	-	-	-	287.0	252.0	115.0	40.0	102.3	-	-	-	-	-	110.0	-	

- * 1. Anteroposterior diameter of horncore at base. 2. Maximum diameter of horncore at base. 3. Approximate height of highest part of horncore base above frontal plane. 4. Anteroposterior diameter of horncore near mid-length. 5. Mediolateral diameter of horncore near mid-length. 6. Thickness of frontal taken in line with middle of horncore base near frontal suture. 7. Length of horncore on lower curve (ridge to tip). 8. Length of horncore on upper curve (base to tip). 9. Maximum distance across orbits. 10. Width at constriction between horncores and orbits. 11. Approximate minimum width between horncore bases. 12. Width at constriction between nuchal crest and posterior of horncores. 13. Height from dorsal margin of foramen magnum to mid-line on dorsal surface of cranium. 14. Height from ventral margin of foramen magnum to top of nuchal crest. 15. Height from dorsal margin of foramen magnum to top of nuchal crest. 16. Height of foramen magnum. 17. Width of foramen magnum. 18. Width across occipital condyles. 19. Basioccipital width (across posterolateral margins).

** I am grateful to A.V. Sher of the Paleontological Institute, USSR Academy of Sciences, Moscow for allowing me to examine and measure *Præovibos* specimens from Siberia.

Table 101. Measurements of Pleistocene Staudinger's muskox (*Praeovibos prisca*) referred metacarpals from the Yukon Territory compared to *Praeovibos* (referred) metacarpals from Siberia.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
<i>Praeovibos prisca</i> (referred). Pleistocene, Y.T.							
NMC 28129 Old Crow Loc. 126	193.9	59.3	37.8	39.6	26.2	65.4	37.4
NMC 16199 Old Crow Loc. 45	184.0e (173.5†)	-	-	37.2	23.3	64.0e	-
<i>Praeovibos</i> sp. (referred). Pleistocene, Siberia**							
"OKC-75-254"	212.8	60.9	37.1	41.0	26.2	65.6	34.8
"26-231"	194.5	56.0	38.8	41.7	25.2	68.7	37.1
"OKC-73-255"	186.8	52.5†	32.4	34.7	21.5	60.2	31.1
"836-95" 47	184.4	58.6	37.7	38.3	22.9	66.4	35.2
"3347-635"	180.8	59.4	39.0	38.8	23.2	70.0	36.7
"3011"	176.2	56.0	37.4	38.0	21.7	66.2	33.6
"3100-597"	173.5	55.8	35.0	38.5	24.4	61.4	33.1
"835-29" 19	171.0	53.3	35.2	36.9	21.7	61.7	32.9

* 1 - Total length.

2 - Proximal width.

3 - Proximal depth.

4 - Midshaft width.

5 - Midshaft depth.

6 - Distal width.

7 - Distal depth.

** A.V. Sher of the Paleontological Institute, USSR Academy of Sciences, Moscow, kindly allowed me to examine and measure a series of metatarsals from Siberian Pleistocene deposits referred to *Praeovibos*, which were not officially cataloged.

specimen reads: "*Ovibos moschatus*, Gmel. Sp. Porcupine River, Arctic America. Pres'd. by the Revd. R. McDonald 1873." The exact locality is unknown, but it is almost certainly from the upper part of the Porcupine River system. It is the most complete specimen known of Staudinger's muskox from Canada. Features that characterize both *Praeovibos priscus* and BM(NH) M 44070 are: (a) the broad, smooth channel between the horncore bases; (b) the relatively narrow anteroposterior diameter of the horncore bases compared to *Ovibos*; (c) the great height of the horncore bases above the frontal plane — particularly near their posterior margins; (d) the narrow, flat frontal region between the flaring horncores and orbits; (e) the flare of the horncores (approximately 55° below the frontal plane), which lies between that of *Symbos cavifrons* and *Ovibos moschatus*. Three supraorbital foramina are present. The basioccipital is shield-shaped with well marked basilar tubercles directed anteriorly toward the mid-line of the cranium at an angle of approximately 30° . The basioccipital has a poorly developed median ridge that becomes a trough between the anterior ends of the basilar tubercles. This specimen and all other cranial and horncore fragments described here differ from *Praeovibos beringiensis* — the only other recognized species — in the shorter anteroposterior diameter of the horncore bases, and their rounder upper profile when viewed from the side. I am grateful to

A.J. Sutcliffe of the British Museum (Natural History) in London for allowing me to examine the original specimen, and for supplying a cast (NMC 13750) of it.

NMC 28100 from Old Crow Locality 109 consists of most of the occipital region and the posterior half of the basioccipital. Because of the small size of the occiput compared to *Ovibos*, and the fact that it matches closely the occipital region of BM(NH) M 44070, I tentatively refer it to *Praeovibos priscus*. The well developed posterior protruberances of the basioccipital suggest that an adult is represented. The fossil is deeply iron-stained, and like the remainder of the specimens described is probably of pre- late Wisconsin age.

The following horncore fragments are referred to males of *Praeovibos priscus*. The larger specimens are similar in size to the *Praeovibos priscus* cranial fragment GIN $\frac{741-1}{109}$ from the Kolyma River, Siberia; apparently slightly smaller than the type of *Praeovibos priscus* from Bad Frankenhausen, Germany; and much smaller than a massive cranium from Siberia "OCX-73-761" (Table 100). To my knowledge, there are no qualitative differences among the Canadian, Siberian and European fossils; therefore the Yukon specimens are referred to *Praeovibos priscus*.

NMC 20135 from Old Crow Locality 74 is the proximal half of a large left horncore attached to part of a frontal. The break on the frontal exposes a section of the bone near the cranial axis. Bone near the anterior margin of the horncore is 25.5 mm thick; that near the posterior margin of the horncore is 35.5 mm thick. The coarse grooving along the length of the horncore is subdued by erosion. The large size of the fossil suggests that an old male is represented.

NMC 27215 from Old Crow Locality 29 is the proximal half of a large left horncore attached to part of a frontal. Bone on the inner margin of the horncore base is deeply pitted, unlike the relatively solid surface of NMC 20135. The frontal bone is thinner: 14.2 mm thick near the anterior margin of the horncore, and 23.0 mm thick near the posterior margin of the horncore. I suggest that this fossil represents a male in early adulthood. The outer surface of the horncore is heavily eroded.

NMC 20607 from Old Crow Locality 20 is a left horncore fragment with part of an attached frontal. It differs in no substantial way from NMC 27215, except that a small part of the posterior margin of the horncore base has been broken away. A large pneumatic cavity is exposed below the base of the horncore. NMC 20891 from Old Crow Locality 3 is a heavily eroded anteroproximal fragment of a left horncore attached to part of the braincase. Evidently it was derived

from a male. It is too poorly preserved to be worth measuring. NMC 23057 from Old Crow Locality 11A is a fragment of the right horncore attached to part of the frontal. The posterior quarter of the horncore base is lacking. The pneumatic cavity at the base of the horncore is clearly exposed. It extends 59 mm from a point below the horncore base into the proximal portion of the horncore, and has an anteroposterior diameter of 41 mm. The specimen is heavily permineralized, being reddish-black.

The following horncores and horncore fragments are tentatively referred to females of *Praeovibos priscus*. The few measurements that are comparable between them and specimens referred to females of Staudinger's muskox by Sher (1971, p. 217; personal communication 1973) are similar (Table 100). I wish to point out that a frontal fragment with attached horncores (GIN $\frac{851-77}{8}$) referred to "presumably a female" of *Praeovibos* from Siberia possesses rather poorly formed horncores, resembling those of an immature tundra muskox. Indeed, Sher (1971, p. 217) remarks: "...the body of the core is very irregular, with tuberosities and foramina", and "relief on the surface of cores weaker and developed only in individual places." Also, the frontal suture is open, suggesting that a subadult is represented. This does not deny the possibility that the specimen represents a female, but it could also belong to an immature male. The Yukon

fossils are quite uniform in size and shape, being slightly less than half the size of the horncores attributed to males, and having thinner braincases. The small size of these horncores, compared to those of referred males, parallels the relationship between females and males of *Ovibos moschatus*. The strong development of surface grooves in the better preserved horncores contrasts with the poorly formed appearance of subadult *Ovibos* horncores; therefore, they are considered to represent adults.

NMC 20540 from Old Crow Locality 22 is a well preserved, complete right horncore attached to a fragment of braincase. The surface sculpture is clear. The largest grooves on the medial surface of the horncore lie nearest to its anterior border. NMC 27749 from Old Crow Locality 66 consists of proximal half of a left horncore attached to part of the braincase. The flatness of the frontal anterior to the horncore base, readily seen in the large cranial fragment BM(NH) M 44070, is observed in this specimen. The horncore has been smoothed by erosion. There is a deep pit approximately 20 mm from the horncore base on its lateral surface. A similar pit is seen about 31 mm from the horncore base in NMC 20540.

NMC 15271 from Old Crow Locality 22 is a complete left horncore attached to a small part of the braincase.

Six deep grooves are apparent on the lateral surface of the horncore, the deepest groove on the medial surface being near the anterior margin as in NMC 20540. NMC 19007 from Old Crow Locality 66 is the proximal part of a left horncore attached to a small portion of the braincase. It is heavily eroded and smaller than the other specimens that I tentatively refer to females of *Praeovibos priscus*.

NMC 28129 from Old Crow Locality 126 is a complete right metacarpal that matches well those in the upper range of *Praeovibos* (Table 101). The non-articular pit on the proximal articular surface is curved as in *Ovibos*. There is a well marked groove on the medial side of the posterior surface of the shaft that is evident in *Ovibos* but not in *Bison*. The specimen can also be differentiated from *Bison* by the fact that it flares less at the proximal and distal ends when viewed from the front. Also, the shaft widens gradually toward the distal end as in *Ovibos* but not as in *Bison*. NMC 28129 is more slender and approximately 12% longer than metacarpals of *Ovibos moschatus* (e.g. NMC 23579). It is referred to *Praeovibos priscus*. NMC 16199 from Old Crow Locality 45 consists of most of a right metacarpal that has been deeply gnawed by a carnivore on the distal articular surface. The proximal end has been broken off. The specimen has the same basic shape as *Ovibos* metacarpals,

but is obviously longer and more slender. In these characters it approaches a cast of a left metacarpal (NMC 31021) from the Kolyma Lowland of Siberia, and the middle of the range of a series of uncataloged metacarpals from Siberia (Table 101), which Sher (personal communications 1973, 1976) refers to *Praeovibos*. NMC 16199 is tentatively referred to *Praeovibos priscus*, keeping in mind that it may also resemble a metacarpal of *Symbos cavifrons*, none of which is available for comparison. The fossil is stained brown.

Discussion

Praeovibos priscus fossils have not been found *in situ* in thick sections in the Old Crow Area, and therefore no estimate of their age can be made on stratigraphic grounds. The dark staining of all of the specimens, and signs of deep penetration of iron oxide to the interior bone of a few, suggest that they are of pre- late Wisconsin age. *Praeovibos* has not been identified from Pleistocene deposits south of Eastern Beringia.

In Alaska, five incomplete crania with horncores and two fragmentary specimens doubtfully referred to *Praeovibos* have been identified by C.E. Ray. The five definitely identifiable specimens are from Cripple Creek sump, and one of the other fragments is from Gold Hill. They are probably Illinoian in age according to

Péwé (1975a, p. 95). The last fragment, from Lower Cleary Creek, may be either of Illinoian or Wisconsin age. Possibly *Praeovibos priscus* is an indicator of Illinoian age in Eastern Beringia.

In Siberia, *Praeovibos priscus* was first identified by E.A. Vangengeim from specimens collected at Krasnoyarka on Irtysh River in western Siberia (Vangengeim and Zazhigin 1965). This locality forms a link between places where *Praeovibos* fossils have been found in northeastern Siberia to the east, and those of Europe to the west. Since then, *Praeovibos priscus* fossils have been reported from the lower part of the Kolyma River, and specimens referred to *Praeovibos* cf. *priscus* and *Praeovibos beringiensis* have been reported from the Krestovka and the Bolshaya Chukochya rivers, respectively - all in the Kolyma Lowland (Sher 1971, p. 218). The type specimen of *Praeovibos beringiensis*, a relatively complete cranium, was derived from sandy loam of the Olyor Suite of Mindel (?Kansan) age. A phalanx from the Lyakhovskiy Islands may be referable to *Praeovibos* (Sher 1971, p. 226).

Fossil remains of *Praeovibos priscus* are recorded from eight localities in Europe (Kahlke 1964, pp. 3-4): (a) late Elster or Mindel II (?late Kansan) gravels at Bad Frankenhausen, Germany - the type locality; (b) sands of Mindel II (?late Kansan) age at Mosbach, Germany.

I agree with Sher (1971, p. 216) that the cranium from this locality, the type of "*Praeovibos schmidtgeni*", lies within the range of variation of *Praeovibos priscus*; (c) sands suggested to be of "Early Middle Pleistocene" age at Bielszowice, Poland; (d) the lowermost layers of Pocket 718 of ?late Mindel I (?early Kansan) age at Koneprusy, Czechoslovakia; (e) a bone-breccia suggested to be of "Early Middle Pleistocene" age at Stranska skala near Brno, Czechoslovakia; (f) possibly the Cromer Forest Bed at Trimingham, England; (g) probably the Cromer Forest Bed at Walcot, England; (h) the Cromer Forest Bed at Eccles, England. The last three fossils are from Cromerian deposits (in the broad sense; see Bishop 1974, p. 312), and I suggest they are from the Beestonian cold phase deposits within the Cromer series (West 1968, pp. 246-249). Hopefully, *Praeovibos* specimens will be found *in situ* in beds along the Norfolk coast in the future. Heavy storm waves used to cause much coastal erosion, promoting the study of early middle Pleistocene vertebrate remains washed out of the high bluffs. Now coastal conservation measures, including extensive breakwaters, allow the faces of the bluffs to slump and become consolidated by vegetation, ironically resulting in a dearth of new paleontological knowledge.

Praeovibos probably originated in northern Eurasia, and may have shared ancestors with *Symbos*. *Praeovibos priscus* spread westward to Poland, Czechoslovakia, and Germany during the Mindel (?Kansan). I suggest the species reached England about that time, crossing a broadened isthmus from France and the Netherlands under periglacial environmental conditions (Flint 1971, p. 774). Staudinger's muskox also spread eastward to the Kolyma Lowland during the Mindel (?Kansan). *Praeovibos beringiensis*, with its distinctly *Ovibos*-like horncores and broad frontal region, seems to be transitional between *Praeovibos priscus* and *Ovibos moschatus*. I suggest that the transition occurred in northern Siberia during the late Mindel (?late Kansan), and doubt that *Ovibos* specimens at Süssenborn are as early as Mindel in age. In this respect, Sher (1971, p. 225) states: "It should also be mentioned that Süssenborn is a site with several horizons of different age... It is not ruled out that the *Ovibos* skull and metacarpals came from horizons of different age in the Süssenborn section." *Praeovibos priscus* may have crossed the Bering Isthmus during the Kansan glaciation, reaching central Alaska and the northwestern Yukon Territory, but Péwé (1975a, p. 95) considers it most likely that all Alaskan fossils are derived from sediments of the following (Illinoian) glaciation. I suggest that the Yukon fossils may be as old as Kansan or as young as Illinoian. *Praeovibos* specimens

appear to be indicators of middle Pleistocene deposits.

It is difficult to understand why *Praeovibos* did not reach southern North America. Perhaps *Symbos cavifrons* (which burgeoned then and was evidently well adapted to steppe or parkland habitat) resulted in its exclusion by being more finely attuned to the warmer habitat farther south. In Eastern Beringia, a reason must be found for its apparent extinction at the close of the Illinoian glaciation. Was it a result of *Praeovibos* giving way to its better-adapted offshoot the tundra muskox *Ovibos moschatus*?

Compared to the tundra muskox, Staudinger's muskox, like *Symbos cavifrons*, was taller and more slenderly built, with a long snout. Its tubular orbits may indicate the presence of a thick coat (see the previous section on *Symbos cavifrons*), suggesting cold-adaptation. Paleoenvironmental evidence supports that suggestion. *Praeovibos priscus* remains have been found in periglacial sediments in Germany, and the species evidently lived under tundra-like conditions in northeastern Siberia. In central Alaska the species seems to have thrived in a cool, loess-steppe environment. Rootlet impressions are seen on the nasals of the type

specimen of *Praeovibos beringiensis* (Sher 1971, Plate 20); I suggest they indicate that the animal died in grassland surroundings. The rather high, narrow hornbases, which lie to the sides of the frontals, suggest to me that Staudinger's muskoxen were not well adapted for butting, and possibly not so sophisticated in herd interactions and co-operation as are the living tundra muskoxen – or perhaps as were the helmeted muskoxen (*Symbos cavifrons*). Probably *Praeovibos priscus* was mainly a grazer, but it may have browsed extensively. Wolves were probably its main predator. *Canis lupus mosbachensis* was a member of several faunas that included Staudinger's muskox (Kahlke 1973). Cave lions and American lions may also have preyed on this species.

Ovibos moschatus (tundra muskox)

Eleven cranial fragments (one from Camden Bay, Alaska) and six complete metapodials (one from Norton Sound, Alaska) of the tundra muskox are described (Figures 90A-C, Tables 102-103). Approximately 40 cheek teeth (mainly from Old Crow Localities 29, 66, 11A and 14), vertebrae and fragments of limb bones representing *Ovibos moschatus* are also in the collection of Yukon Pleistocene mammals. *Ovibos* fossils are of particular



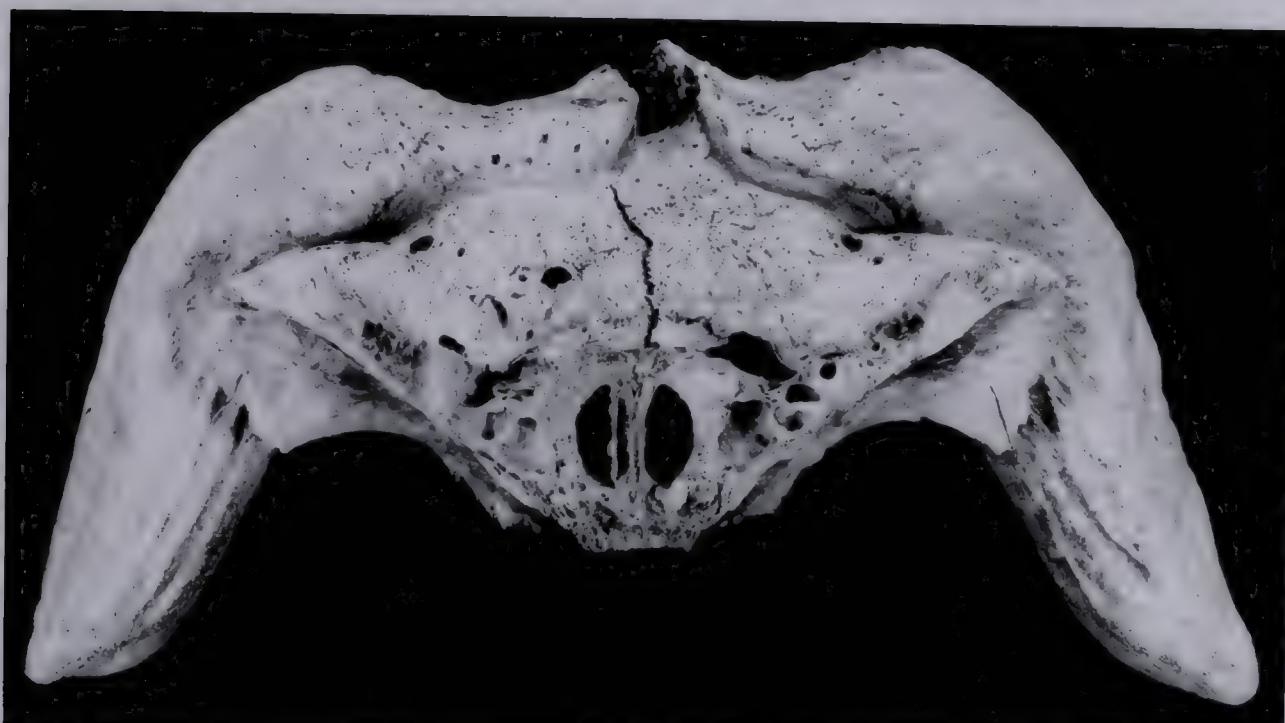
Figure 90. Posterior cranial fragment with horncores
(NMC 17678, Herschel Island Locality 3)
of a Pleistocene tundra muskox (*Ovibos*
moschatus).

- A. Dorsal view (anterior to bottom).
- B. Anterior view.
- C. Ventral view (anterior to bottom).



A

5 CM



B

5 CM



C

5 CM

Table 102. Measurements of Pleistocene tundra muskox (*Ovibos moschatus*) crania from the Yukon Territory and Alaska compared to those of Recent *Ovibos moschatus* from North America.

Specimens	Measurements (mm)*														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Ovibos moschatus</i> . Pleistocene, Y.T., Alaska															
<u>Males</u>															
NMC 15267 Old Crow Loc. 22	158.5	56.0	-	-	-	-	140.9	100.0	80.1	99.5	30.3	32.0	101.6	181.8	64.9
F:AM 34609 Dominion Ck. (Dawson Area)	210.0	-	-	-	168.4	-	151.4	-	81.8	112.7	29.9	29.9	-	201.6	74.6
NMC 17678 Herschel Loc. 3**	225.9	84.0	183.0	305.0	143.7	352.0	147.5	-	-	-	-	-	-	-	-
NMC 18034 Old Crow Loc. 11a	173.0	71.7	-	-	143.3	-	124.0	-	-	-	-	-	-	-	-
NMC 28200 Old Crow Loc. 131	-	-	-	-	-	-	-	-	87.3	111.4	26.5	29.2	130.0	-	72.6
NMC 20477 Old Crow Loc. 20	-	-	-	-	-	-	-	-	-	-	32.9	30.0	112.0a	-	63.7
NMC 2460 Camden Bay, Alaska	173.1	66.6	122.0	242.0	150.8	217.3	129.9	115.9	76.7	99.2	30.1	31.8a	117.1	172.7 ⁺	66.6
<u>Females</u>															
OCR 1175-1-9 Old Crow Basin	82.5	47.4	96.0	197.0	107.2	230.6	100.9	86.7	80.7	105.5	28.9	36.8	122.0e	160.0	55.4
NMC 14707 Old Crow Loc. 28	62.9	43.3	-	-	-	-	-	-	-	-	-	-	-	-	-
NMC 20601 Old Crow Loc. 20	64.5e	39.5 ⁺	-	-	104.0e	-	-	-	-	-	-	-	-	-	-
<i>Ovibos moschatus</i> . Recent, N. America															
<u>Males</u>															
NMC uncataloged (from mounted skeleton)	192.0	72.4	162.0	280.0	134.4	297.7	133.1	106.2	77.8	103.5	27.3	30.8	107.5	180.7	-
NMC 23320 Prince of Wales I., N.W.T.	204.7	64.4e	165.0	270.0	157.9	267.6	134.6	108.1	75.5	103.9	33.3	34.0	112.7	188.8	72.2
NMC 23297 Prince of Wales I., N.W.T.	192.1	75.2	-	-	151.2	-	133.4	107.8	84.0	110.0	36.4	37.9	120.2	186.3	71.2
NMC uncataloged Lookout Pt., N.W.T.	191.2	81.0	144.0	270.0	132.1	288.7	127.5	116.8	83.7	109.9	27.7	29.4	111.2	172.1	62.1
NMC 34437 Beverly L., N.W.T.	184.8	68.9	-	-	144.6	-	134.2	116.1	75.4	103.0	30.0	31.7	110.0	186.0	66.2
NMC 34438 Thelon L., N.W.T.	190.8	72.2	-	-	145.1	-	140.5	130.0	81.7	109.8	27.7	25.5	-	186.7 ⁺	61.4
NMC 36295 Ellef Ringnes I., N.W.T.	198.7	68.6a	151.0	260.0	143.9	-	123.6	96.8	81.5	104.0	30.2	28.9	110.0	175.5	68.5
NMC uncataloged Falcon Ck., N.W.T.	198.9	70.3e	167.0	268.0	135.3	-	130.2	111.1	82.7	108.9	28.1	32.9	-	184.8	63.3
NMC 23322 Prince of Wales I., N.W.T.	174.3	64.2a	150.0	270.0	154.9	-	121.4	103.2	80.1	103.9	29.6	30.6	120.3	174.2	63.9
<u>Females</u>															
NMC 26478 N.W.T.	62.0a	-	-	-	122.8	-	106.4	116.2	79.6	102.9	24.3	30.6	100.2	148.6	55.3
NMC 22059 Prince Patrick I., N.W.T.	51.0a	-	-	-	124.4	-	93.3	82.0e	74.2	101.2	33.4	40.7	112.4	147.6	57.5

* 1 - Anteroposterior diameter of horncore at base (maximum).

2 - Dorsoventral diameter of horncore on lower curve (ridge to tip).

3 - Length of horncore on lower curve (ridge to tip).

4 - Length of horncore on upper curve (middle of horncore base to tip).

5 - Width of cranium at constriction between horncores and orbits.

6 - Minimum width between horncore tips.

7 - Width of cranium at constriction above nuchal crest.

8 - Height from dorsal margin of foramen magnum to mid-line on dorsal surface of cranium.

9 - Height from dorsal margin of foramen magnum to top of nuchal crest.

10 - Height from ventral margin of foramen magnum to top of nuchal crest.

11 - Height of foramen magnum.

12 - Width of foramen magnum.

13 - Minimum width across occipital condyles.

14 - Maximum width of cranium above auditory meatus.

15 - Basioccipital width (across posterolateral margins).

**Tentatively referred to *Ovibos moschatus*.

Table 103. Measurements of Pleistocene tundra muskox (*Ovibos moschatus*) metapodials from the Yukon Territory and Alaska compared to those of Recent *Ovibos moschatus* from North America and Greenland.

Specimens	Measurements (mm)*						
	1	2	3	4	5	6	7
Metacarpals							
<i>Ovibos moschatus</i> .							
Pleistocene, Y.T.							
NMC 13592 Old Crow Loc. 11A	169.8	54.1	33.0	37.5	20.5	68.2	33.1
NMC 23579 Old Crow Loc. 11A	170.0	55.6	35.3	41.4	21.8	65.7	34.8
NMC 29186 Sixtymile Loc. 3	162.8	55.1	34.5	37.4	21.1	65.8	33.8
<i>Ovibos moschatus</i> .							
Pleistocene, Alaska							
NMC 6758 Norton Sound	169.6	57.3	37.9	42.8	24.3	67.4	34.4
<i>Ovibos moschatus</i> .							
Recent, N. America, Greenland							
NMC uncataloged Canada	178.6a	54.6	35.5	36.6	21.3	66.0	29.3a
ZIN 8690 Canada (Sher 1971, Table 36)**	149.4	49.7	31.2	31.4a	17.3a	57.5	31.0
ZIN 27296 Greenland (Sher 1971, Table 36)**	154.0	56.0	37.1	37.0a	20.7a	65.0	34.4
Metatarsals							
<i>Ovibos moschatus</i> .							
Pleistocene, Y.T.							
NMC 29185 Sixtymile Loc. 3	194.3	48.0	43.8	32.7	28.0	63.7	35.4
NMC 22505 Old Crow Loc. 45	185.8	43.5	37.4	30.2	23.3	55.5	33.2
<i>Ovibos moschatus</i> .							
Recent, N. America, Greenland							
NMC 33549 Canada	180.0	46.5	41.5	29.6	25.1	58.2	34.4
NMC uncataloged Canada	188.0a	45.6	40.6	27.7	26.3	58.6	35.5a
ZIN 8690 Canada (Sher 1971, Table 39)**	156.0	39.8	37.0	23.0a	23.0a	51.0	29.5
ZIN 27296 Greenland (Sher 1971, Table 39)**	163.0	45.0	43.0	28.0a	24.0a	56.5	32.0

* 1 - Total length.
2 - Proximal width.
3 - Proximal depth.
4 - Midshaft width.

5 - Midshaft depth.
6 - Distal width.
7 - Distal depth.

**Sher seems to have measured total length from the main proximal articular surface, rather than on the most proximal projection of the metapodial, as I have done.

interest and importance because they are reliable indicators of tundra-like, or more rarely, cold loess-steppe environments.

Referred specimens

The following specimens are referred to adult males. NMC 15267 from Old Crow Locality 22 consists of a badly damaged posterior cranial fragment. Only stubs of the horncores are preserved, bone is lacking anterior to the horncore bases, and a large part of the upper occipital region, including the posterior part of the left horncore base, is missing. The basioccipital area is intact. The fossil is readily referred to an adult male of *Ovibos moschatus*, for large horncore bases cover most of the upper surface of the braincase, leaving a narrow median groove between them. The specimen is stained dark reddish brown. F:AM 34609, a large cranium with partial horncores of *Ovibos moschatus*, was collected at Dominion Creek in the Dawson Area in 1948. I am grateful to M.C. McKenna and M.F. Skinner for allowing me to examine and measure the specimen, which is preserved in the Frick Collection at the American Museum of Natural History in New York.

NMC 17678 from Herschel Island Locality 3 is the upper half of a posterior cranial fragment with complete, massive horncore bases. Bone is lacking anterior to the

orbits. Heavily eroded upper parts of the orbits are preserved. The median groove between the horncore bases is deep. The specimen can be referred with confidence to *Ovibos*, but the massiveness of the horncores and the great spread between their tips are not typical of most male *Ovibos moschatus* crania I have seen. Therefore, NMC 17678 is only tentatively referred to *Ovibos moschatus*. The dark staining of the fossil suggests a pre- late Wisconsin age. V. Stefannson (Allen 1913, pp. 720-721) and R.M. Anderson (Allen 1913, pp. 186-187) mention that a skull of *Ovibos moschatus* was found on Herschel Island in 1908. Through the courtesy of K. Djukastein, a miner in the Dawson Area, I have been able to examine, measure, and sample for radiocarbon analysis an upper, posterior cranial fragment from Brewer Locality 1. Most of the right horncore and the stub of the left horncore are preserved, in addition to the upper parts of both orbits. The dorsal surfaces of the horncore bases are stream eroded. NMC 18034 from Old Crow Locality 11A is the upper half of a posterior cranial fragment. Most of the bone anterior to the horncore bases is lacking. The median groove between the horncore bases is slightly concave anteroposteriorly, and pitted centrally. The bone is stained rusty brown. NMC 2460 was collected from a "black earth sea cliff" on Camden Bay (10 miles (16 km) east of

Collinson Point) by E. de K. Leffingwell in 1914. It consists of the posterior part of a cranium with complete horncores. Bone is lacking anterior to the orbits (of which only the posterior margins are preserved). The lateral margins of the occipital region and the occipital condyles are eroded. The large horncore bases and the high degree of suture fusion indicate that the fossil represents a male in late adulthood. NMC 2460 is stained dark brown. NMC 28200 from Old Crow Locality 131 consists of the occipital and basioccipital parts of a cranium. The lateral margins of the occiput are strongly eroded. The great breadth of the basioccipital suggests that an adult male is represented (Harington 1964, p. 85). NMC 20477 from Old Crow Locality 20 is a heavily eroded posterior cranial fragment comprising part of the ventral half of the occiput, the basioccipital and portions of the pterygoid crest. The surface of the fossil is oxidized, being stained orange brown. The large basioccipital breadth suggests that a male is represented. The morphological features of the basioccipital (e.g. the shield shape, with the posterior channel becoming a ridge centrally and a channel again at the anterior end) match those of *Ovibos moschatus*.

The following specimens are referred to adult

females. OCR 1175-1-9 from an unknown locality in the Old Crow Basin is a posterior cranial fragment with complete horncores. Bone anterior to the orbits, and in the region of the right occipital condyle is lacking. The relatively well developed horncore bases compared to Recent females of tundra muskoxen, the pronounced grooves paralleling the length of the horncores, and the obliteration of the frontal suture indicate that the fossil represents an extremely old female. In every morphological detail preserved, OCR 1175-1-9 corresponds to the same part of a modern female tundra muskox skull (e.g. NMC 26478). However, the width of the cranium between horncore and orbit seems unusually small (Table 102). Sex is readily determined by the wide (27 mm) space between the horncore bases (typical of females) compared to the narrow median grooves that separate the more massive horncore bases of adult male tundra muskoxen. The anteroposterior narrowness of the horncores compared to those of male tundra muskoxen, and the narrowness of the basioccipital also suggest that the specimen represents a female. The bone is stained brown.

NMC 14703 from Old Crow Locality 28 is a left horncore fragment attached to part of the braincase. The

distal half of the horncore, and part of its posterior edge, are missing. The shape of the horncore base and the broad space that obviously existed between horncore bases indicate clearly that the fossil was derived from a female. The horncore base is smaller than that of OCR-1175-1-9, so NMC 14703 may represent a younger adult female. The bone is stained brown. NMC 20601 from Old Crow Locality 20 consists of three-quarters of a heavily abraded and weathered left horncore attached to the left half of the braincase. The surface of the specimen is oxidized.

Despite a few fundamental differences, the striking similarity of females of *Ovibos moschatus* to males of *Praeovibos priscus* is evident when the fossils are studied in sequence, prompting the thought that females among the low-horned muskoxen such as *Ovibos* and *Symbos* may be closer in appearance to their ancestors than the males, whose massive hornbases are exaggerated secondary sexual characteristics.

Three complete metacarpals from the Yukon and one from Alaska are referred to *Ovibos moschatus*. NMC 13592 from Old Crow Locality 11A is a left metacarpal. NMC 23579 from the same locality is a right metacarpal. Both are stained brown, and compare well with Recent

tundra muskox metacarpals. NMC 29186 from Sixtymile Locality 3 is a complete right metacarpal. It is slightly smaller than the others. The bone is pale tan and has a fresh appearance. I suggest it is of late Wisconsin age. NMC 6758, a right metacarpal from Norton Sound, Alaska, is included for comparative purposes. It is similar in size to NMC 23579 from Old Crow Locality 11A. It is stained dark brown and, like NMC 13592 and 23579, is presumably older than late Wisconsin.

Two complete metatarsals are referred to *Ovibos moschatus*. The larger, NMC 29185 from Sixtymile Locality 3, is pale buff and fresh in appearance. It is probably of late Wisconsin age. NMC 22505 from Old Crow Locality 45 is smaller. It is stained dark brown and is probably pre- late Wisconsin in age.

Discussion

Tundra muskox fossils are widespread in the Yukon Territory, having been found in the Stewart River (Brewer Creek), Dawson, Sixtymile, Old Crow and Herschel areas. According to their dark staining, I suggest that most of the Yukon tundra muskox fossils are of pre- late Wisconsin age. NMC 16155, an unworn ovibovine LM² from Unit 2 at Old Crow Locality 44 probably represents

Ovibos moschatus. If so, it indicates that tundra muskoxen occupied the Old Crow Basin more than 54,000 years ago. The fresh looking metapodials from Sixtymile Locality 3 are probably of late Wisconsin age (Harington 1976 MS., pp. 63-64). Unspecified "muskox" (presumably *Ovibos moschatus*) bones from the upper part of humic sands at Engigstciak near the mouth of Firth River, may be about 3,250 years old (Mackay *et al.* 1961, p. 34). The cranial fragment from Brewer Creek indicates that tundra muskoxen lived south of the Dawson Area as late as approximately 2,800 years ago. The species no longer occurs naturally in the Yukon, but in July 1969 two muskoxen were sighted near King Point on the Yukon coast. They came from a "seed" herd introduced from Nunivak Island to the arctic coast of Alaska opposite Barter Island in April 1969 (Youngman 1975, pp. 169-170).

In other parts of Canada, mainly skull fragments of *Ovibos moschatus* have been recorded from: Ontario (eastern Toronto - the type of "*Ovibos proximus*" (Bensley 1913), now considered to be a junior synonym of *Ovibos moschatus* (Harington 1970b, p. 3); northwestern Toronto, from bar deposits of probable late Wisconsin age); Manitoba (Grandview - a cranial fragment radiocarbon dated at $8,620 \pm 190$ years B.P. (I-1623) (Harington 1970b));

Alberta (Ponoka, Edmonton, Cold Lake); and the Northwest Territories (Bernard River, Banks Island - a metacarpal fragment radiocarbon dated at >34,000 years B.P. (S-288) (Maher 1968, p. 261); Thesiger Bay, Banks Island - a pelvic bone from peat radiocarbon dated at $10,660 \pm 170$ years B.P. (GSC-240); near Alert, Ellesmere Island, from raised beaches probably of early postglacial age).

In the conterminous United States, approximately 12 cranial fragments of *Ovibos* are known from Illinois, Indiana, Iowa, Minnesota, Montana, Nebraska, New York, Ohio, South Dakota, and possibly West Virginia. Probably most specimens are of Wisconsin age; however, fossils from near Morrill, Nebraska, and Jinks Hollow, Illinois may be of pre-Wisconsin age (C.E. Ray, personal communication 1966).

Approximately 70 *Ovibos moschatus* specimens, mainly cranial fragments, are known from Alaskan Pleistocene deposits. The geologically oldest fossils consist of part of a skull from outwash gravels of Illinoian age near Nome in western Alaska, and two specimens from loess at Cripple Creek sump near Fairbanks, which T.L. Péwé considers to be of Illinoian age (Harrington 1970c, p. 1329). Some of the specimens from Gold Hill may be of similar

age. I am grateful to M.C. McKenna and M.F. Skinner of the American Museum of Natural History for allowing me to examine and measure *Ovibos* crania from the Fairbanks area, which comprise most of the fossils. The sites, in descending order of productivity of skull fragments, are: Cripple Creek (21), Engineer Creek (14), Fairbanks Creek (7), Gold Hill (6), Lower Goldstream Creek (5), Little Eldorado Creek (3), Dawson Cut (2), Cleary Creek (2), Dome Creek (1), Fox Creek (1). Other cranial fragments in the Frick Collection at the American Museum of Natural History are from: Elephant Point (Eschscholtz Bay) (3), Inmachuk River (Seward Peninsula) (2), Candle Creek (Eschscholtz Bay) (1), Fish Creek (1), Colville River (1). Additional specimens are known from the Kaolak River, Ikpikpuk River, and Camden Bay (NMC 2460).

Remains of *Ovibos moschatus* are widespread in northern Eurasia (Gromova 1935; Harington 1961, pp. 436-457, Figure 24). For reasons stated previously, I am not convinced that the tundra muskox occupied Europe as early as Mindel I (?early Kansan) (Kahlke 1964, p. 3): better evidence is required to demonstrate that the *Ovibos* material recovered at Süssenborn and Obergünzberg was not derived from units stratigraphically higher and more recent than those of Mindel (?Kansan) age. I suggest that there is evidence of a transition from *Praeovibos priscus* via *Praeovibos beringiensis* to *Ovibos* sp. toward the close of the

Mindel (?Kansan) glaciation in northern Siberia (e.g. Olyor Suite). A large cranium with heavy, high-rising horncore bases, with exostoses, but without the usual fossae may date to the end of the transition period. It was collected on the Upper Ob River (Sher 1971, p. 227). A well preserved skull from Rublevo south of Moscow is larger than late Pleistocene tundra muskoxen, and differs from them in proportions. The animal represented by this fossil probably lived near the edge of the advancing Dniepr ice (Saale = Illinoian (Flint 1971, p. 629)). NMC 17678 from Herschel Island, Yukon Territory, with its massive horncore bases and relatively large spread from tip to tip of the horncores, may have affinities with the Upper Ob and Rublevo fossils. Evidently the first major dispersal of tundra muskoxen occurred during the early Riss (early Illinoian) glaciation. *Ovibos moschatus* is not recorded in any of the major Siberian Pleistocene mammal faunas prior to Riss (Illinoian) time. The species is a member of the late Pleistocene (Illinoian to Wisconsin?) fauna from Bolshoi Lyakhov Island (Vangengeim 1961), and tundra muskox remains are known from the early Wisconsin Iedoma Suite in the Kolyma Lowland (Sher 1971), and from late Pleistocene (?Wisconsin) deposits at Proliv Dmitriya Lapteva (Vereshchagin 1974). Vangengeim (1961, p. 145) remarks that the first appearance of the muskox in northeastern Siberia was during "the first stages

of the maximal {Illinoian} glaciation," and that it was very common in Siberia from that time until the early postglacial.

Andrée (1933) discusses an interesting sample of European *Ovibos moschatus* remains. Of 28 tundra muskox occurrences in Germany, eight specimens are from Saale (Illinoian) deposits and 15 are from Weichsel (Wisconsin) sediments — presumably the remainder could not be dated stratigraphically. Soergel's (1942, p. 79) important study of the distribution of Pleistocene tundra muskoxen in Europe led him to conclude that "the deposits in which remnants of muskoxen are found show that they were common over central Europe only during glacial periods..." Evidence (E. Alendal, personal communication 1976; Heintz 1962, p. 208; Heintz and Garutt 1965, p. 78) indicates that muskoxen and woolly mammoths migrated to Scandinavia during the interglacials of the late Pleistocene. Reynolds (1934, p. 10) notes that *Ovibos moschatus* occurred in various parts of Europe in Mousterian deposits of early Weichsel (early Wisconsin) age, but states, "It is not until late Palaeolithic (Magdalenian) times, when the tundra animals both in Europe and N. America spread far to the south, that *Ovibos* became a really characteristic member of the fauna." The southern limits of *Ovibos moschatus*

in Eurasia, from west to east are: Dordogne, France; Lake Constance, Switzerland; Hungary (46°N); Kostienki (Don River, 51°N), and Lake Baikal, U.S.S.R. (Harington 1961, p. 150).

Prior to summarizing the dispersal history of *Ovibos moschatus*, I wish to comment generally on the origins of muskoxen and their evolutionary history. In 1961, I (Harington 1961, pp. 97-99) proposed an "Ontogenetic - Phylogenetic" hypothesis in an attempt to explain various stages in the evolutionary history of the muskoxen (Tribe Ovibovini). According to this hypothesis, the earliest muskoxen would have had high, small horns (like the "spikes" of young *Ovibos moschatus*), later evolved muskoxen would have had horns lying near the frontal plane (like those of 18-months-old *Ovibos moschatus*), and the most "advanced" forms would have large horns that drop tightly near the cheek bones (like those of adult *Ovibos moschatus*). Other trends in the course of evolution of the muskoxen were considered to be: (a) increasing body size; (b) increasing orbital protrusion and specialization (Harington 1961, pp. 100-102). The increasing degree of orbital projection is particularly noticeable in the later lowland muskoxen, such as *Symbos cavifrons*, *Praeovibos priscus*, and *Ovibos moschatus*. Evidently it

occurred when muskoxen were adapting to colder environments. As mentioned previously, tubular orbits allow for development of thick insulating hair on the head, while maintaining a suitable field of vision. Thus, they promote cold survival and survival by retaining the ability to detect predators readily.

I advance for consideration the suggestion that the Ovibovini be divided into two subtribal taxa: (a) the "alticornis" group, including those genera with horncores lying mainly in the frontal plane, or rising above it (e.g. *Boöpsis*, *Euceratherium* (including *Preptoceras*), *Soergelia*, tentatively *Budorcas*, and possibly some more primitive genera ("stem muskoxen") as yet not clearly recognized as belonging to the Ovibovini); (b) the "depressicornis" group, including those genera with horncores mainly lying below the frontal plane (e.g. *Symbos* (probably including *Boötherium sargenti*), *Parovibos*, *Praeovibos* and *Ovibos*). Such a division may be useful in separating fossils of genera that probably arose during the Pliocene and early Pleistocene (Nebraskan), from those which may have arisen during the Kansan - Illinoian period. Excepting *Soergelia*, this division also seems to be useful in separating upland ("alticornis") muskoxen from lowland-adapted ("depressicornis") muskoxen.

Among a group of Eurasian lower Pliocene bovids

(or "stem muskoxen") that have some affinities with later muskoxen are *Plesiaddax*, *Urmiaatherium* and *Parurmiatherium*. Perhaps it was from an animal belonging to this basic upland stock with rather small, very high horns that the "alticornis" group arose. I suspect that *Budorcas taxicolor*, the takin, which presently survives in a zone extending from subalpine meadows to ground just above the tree-line in southeastern Asia, is an early offshoot of the "stem muskoxen". Evidently it is adapted to life in mountainous or hilly terrain, which may have been typical of early muskoxen, and it survives near the original dispersal centre of the Ovibovini in central Asia. Its horns are relatively high, but twist back near the tips rather than forward as in most muskoxen. *Budorcas* is very much like *Ovibos* in general body structure, and it is tentatively included in the Ovibovini. It is important that comparative serological and chromosome studies (Tietz and Teal 1967, p. 236; Heck *et al.* 1967, p. 178) be carried out on *Budorcas*, so that its relationship with *Ovibos* may be clarified.

Boöpsis, which first occurs in the fossil record in lower Pleistocene sediments (Choukoutien, Locality 9, China), seems to be closer to the phylogenetic line leading to *Ovibos* than is *Budorcas*. So far, *Boöpsis* is

only known from two localities in northeastern China. Probably it diverged from the same stock as *Euceratherium* (including *Preptoceras*) during the Nebraskan glaciation. *Soergelia* also seems to have arisen from this stock. All have horncores on pedicels. The horncores spread laterally, bend forward and rise toward the tips, and generally lie near to or above the frontal plane. The relationships among these three genera deserve careful study. I (Harrington 1961, p. 59) have previously noted the many similarities between *Boöpsis* and *Euceratherium*, but was unable to obtain a cast of *Boöpsis* from China — a necessity for meaningful comparisons. *Boöpsis* evidently became extinct toward the close of the early Pleistocene (?Nebraskan), while its close relative *Euceratherium* presumably moved into North America across the Bering Isthmus during the following Kansan glaciation, quickly spreading southward through the northern Cordillera and reaching California (Irvington) by late Kansan time. *Euceratherium*, like *Budorcas* and possibly *Boöpsis*, was probably adapted to subalpine life, and seems to have partly filled the environmental niche now occupied by North American mountain sheep. *Euceratherium*, which ranged as far south as Mexico, survived in the southern Cordillera of North America until Wisconsin time.

Soergelia appears to be the earliest known muskox adapted to lowland conditions. It may have originated toward the close of the Nebraskan time, dispersing rapidly from northern Asia westward into Europe and eastward across the Bering Isthmus to southern North America (Texas) during the Kansan glaciation. It seems to have been confined to Kansan time; therefore, it is probably a good Holarctic index fossil for that glacial phase in which muskoxen burgeoned and dispersed widely on the expanding steppe grasslands and tundra. I (Harington 1961, p. 129) have suggested that increasing competition from more specialized muskoxen, such as *Praeovibos* in Eurasia and *Symbos* in North America, may have resulted in its extinction.

The affinities and systematic position of *Boötherium bombifrons* are perplexing. To my knowledge no other specimen like the holotype from Big Bone Lick, Kentucky has been found. The species seems to be most closely related to *Soergelia* among known muskoxen. I base this observation on the well-developed longitudinally-grooved, horncore burrs and pedicels, the long, pronounced downslope on the upper surface of the cranium posterior to the horncores, and the smallness of the skull relative to *Symbos* and *Ovibos*. The major difference is in the low position of the horncores. According to Allen (1913, p. 210)

the sutures are fused as in an adult, so presumably it cannot represent a muskox in an early stage of horncore development (e.g. a 3-year-old *Ovibos moschatus* (Allen 1913, Figure 10)), which otherwise would seem most likely.

Symbos, possibly the closely associated genus *Parovibos* (= the type of "*Ovibos recticornis*"), and *Praeovibos* seem to have diverged from the same ancestors as *Soergelia* in early Kansan time. Their horns were bent below the frontal plane, their orbits projected more than those of earlier muskoxen, and they were larger (particularly taller and more slender in the body) than *Soergelia*. Possibly co-operative herd interactions were not so well developed in *Praeovibos* as in *Symbos*, for reasons mentioned previously, which may account for its relatively short life in Eurasia.

Symbos had horncores lying mainly below the frontal plane, but higher than those of *Praeovibos*. It also had less tubular orbits, suggesting that it may have diverged from its *Soergelia*-like ancestors before *Praeovibos* — probably about Kansan time. Possibly *Parovibos recticornis* from "middle Pleistocene" deposits of Radotin, Czechoslovakia represents this type of muskox in Europe. This case deserves careful investigation.

The basioccipital of *Symbos* is wedge-shaped and "channeled" like that of *Soergelia*, rather than being shield-shaped and "ridged" centrally as in *Praeovibos* and *Ovibos*. Like *Praeovibos* and unlike *Ovibos*, *Symbos* had a long muzzle and was relatively tall and slender. There was a parallelism between *Symbos* and *Ovibos* males in the massive concrescence of their horncore bases, which perhaps coincided with a more sophisticated type of group organization. *Symbos* may have differentiated in Asia, reaching Alaska via the Bering Isthmus in early Illinoian time and quickly penetrating to favorable steppe or parkland habitat in south - central North America. It was able to move easily through mountainous country, and survived until the close of the Wisconsin glaciation in North America. Restriction of its natural habitat and the incursions of bison adapted to moister woodland (e.g. the western bison, *Bison bison occidentalis*) conditions may have contributed to its extinction.

There is no doubt that *Praeovibos* was well adapted to tundra-like conditions. Like *Soergelia* it radiated from northern Asia in Kansan time, spreading westward to Europe and eastward to the Kolyma Lowland of Siberia. If it did not reach North America earlier, it crossed to Alaska and the Yukon via the Bering Isthmus during the

Illinoian glaciation. I think that *Praeovibos beringiensis* evolved from *Praeovibos priscus* near the end of Kansan time. *Praeovibos beringiensis*, in turn, seems to have given rise to *Ovibos*. It has many similarities to *Ovibos* in the posterior of the cranium (particularly in the horncores, and position of the orbits), but is much longer and deeper in the muzzle — a "mosaic" type of evolution is postulated in this case. Apparently a shortening and broadening of the extremities, and a broadening of the cheek teeth occurred during the last part of the transition.

I now return to a summary of the dispersal history of *Ovibos*. By Illinoian time, *Ovibos moschatus* had spread westward to Europe and eastward across the relatively dry, cool grasslands of the Bering Isthmus to Eastern Beringia (where it seems to have out-competed the last herds of *Praeovibos priscus* in this marginal area) and possibly to the northern United States (Morrill, Nebraska; Jinks Hollow, Illinois). If *Ovibos* herds reached tundra-like areas south of the Illinoian continental ice, presumably they shifted northward as that ice sheet melted back during the Sangamon interglacial. With subsequent expansion of the Wisconsin ice, muskox herds were probably isolated in refugia on Banks Island, unglaciated areas of Alaska

and the Yukon Territory (Eastern Beringia), and in a narrow, tundra-like belt south of the ice.

Most *Ovibos moschatus* specimens in a zone from Montana to New York are probably of Wisconsin age. In eastern North America (e.g. Vestal, New York; Toronto, Ontario) the species survived until the close of the Wisconsin glaciation. But that region seems to have been a cul-de-sac for muskoxen: they were prevented from dispersing northward to the tundra areas of Ungava by non-accessibility, or lack of sufficient tundra-like range as the Labrador ice sheet melted back. It is important to recognize the rapid replacement of early late-glacial tundra vegetation by open spruce forests or woodlands as the ice sheet retreated from the region (Dreimanis 1967, p. 669). Farther west, however, herds that lived in Iowa, South Dakota, Minnesota and Montana probably were able to follow a narrow tundra-like zone northwestward and northward as Keewatin ice retreated, until they reached their present range in the Northwest Territories mainland. The Grandview specimen indicates that muskox herds ranged the western shore of Lake Agassiz about 8,600 years ago when the ice sheet was not much farther north. It seems to demonstrate the reality of a northward movement of muskoxen from the southern refugium.

Ovibos moschatus fossils from surface gravel deposits near Ponoka and Cold Lake, Alberta may also be of postglacial age. If so, they could represent ancestors of the muskoxen now occupying the tundra north of Great Bear Lake.

Considering the uncertainty of evidence for muskoxen in the Pearyland refugium during the Wisconsin glaciation, the present distribution of muskoxen in the Canadian Arctic Islands is perhaps best explained by postulating a northeasterly and easterly movement from the Banks Island refugium as the Innuitian and Laurentide ice sheets retreated (Blake 1970, pp. 660-661). Dispersal in this region was obviously achieved by herds moving from island to island over sea ice. Prince of Wales Island appears to be a zone of contact between muskoxen from Banks Island and those from the southern refugium (Harrington 1970b, p. 5).

Evidently tundra muskoxen were common and widely distributed in Eastern Beringia during the Wisconsin glaciation. As postglacial warming progressed, muskox range contracted until herds were largely confined to the northern coastal region of Alaska and the Yukon. Yet it is interesting to note that *Ovibos moschatus* survived in the more southerly Stewart River area

(Brewer Creek) until approximately 2,800 years ago. The last muskoxen native to Alaska may have been killed west of Point Barrow about 1858 (Allen 1913, p. 188). I attribute the extinction of tundra muskoxen in Eastern Beringia mainly to a combination of climatic change (from dry and cool to warmer and wetter), which depleted suitable muskox range, and increasingly effective human predation.

A radiocarbon date on tundra muskox cranial bone from Taimyr, the northernmost part of the Siberian mainland, is reported as $3,790 \pm 80$ years B.P. by N.K. Vereshchagin (personal communication 1968), who kindly supplied me with a bone sample from the same cranium. A date of $2,910 \pm 95$ years B.P. (I-4220) was obtained, which confirms the relatively recent extinction of *Ovibos moschatus* in Eurasia.

Ovibos moschatus was Holarctic in distribution during the Wisconsin glaciation, when its range extended from southern England in the west, via Siberia, Alaska and the Yukon Territory to New York in the east. In appearance, the tundra muskox is like a blunt-nosed, extremely large sheep with long, dark hair. It is characterized by whitish horns that bend downward close

to the skull, sweeping forward, upward and outward at the tips. Adult males have large horn bases separated by a narrow median groove, whereas horns of females are relatively poorly developed, with fur growing between the widely separated, smaller horn bases. Whitish "saddle" markings and "socks" also characterize the species. Tundra muskoxen have short legs, necks and tails. Bulls are larger than cows, having a shoulder height of approximately 4.5 feet (1.4 m), and weighing 581 to 1,437 pounds (263 to 650 kg) under natural conditions.

Tundra muskoxen are gregarious, sometimes congregating in herds of hundreds. Average herd size is about 15. Effective social co-operation is seen in the various defense formations assumed when confronted by an attacker or attackers. Highly ritualized butting contests occur between adult males during the rutting period in August. Calves are born in late April or early May, and are very precocious. This species prefers areas of arctic tundra with sparse snowfall and dry, cold winters. Meadows rich in willows, sedges and grasses constitute suitable summer habitat. *Ovibos moschatus* fossils are good paleoenvironmental indicators of tundra, tundra-like or rarely cold, loess-steppe conditions. Their thick pelts, consisting of grayish underwool (qiviut) covered

by long, coarse guard hairs, coupled with short extremities indicate excellent adaptation to cold. The animals browse and graze. Winter food consists mainly of browse such as willows, ground birch, crowberry, and bilberry. In summer, tundra muskoxen feed mainly on fresh willow shoots, sedges, blue grass, fescue and other grasses (Tener 1965; Banfield 1974, pp. 411-413).

Wolves are the main predators of the tundra muskox, but seldom are they able to penetrate the defensive formation of the muskoxen to kill a calf. Often old, or otherwise handicapped muskoxen are attacked and killed — particularly if they are alone. Brown bears sometimes attack muskoxen. Man has been an important predator. Although tundra muskoxen are known to have occurred in southern Europe during the last glaciation, their bones seldom appear in cave middens (Cornwall 1968, p. 188), and they feature rarely in Paleolithic art. A beautiful, free-standing sculpture of a head of a tundra muskox was found in Laugerie Haute (Ucko and Rosenfeld 1967, Figure 35), and a classic figurine of the head and shoulder of a tundra muskox made from cervid antler was found in Kesslerloch Cave near Thainingen, Switzerland (Harington 1961, p. 192, Figure 19). A frieze at Le Roc, depicting a man being charged by a

muskox, probably records an incident that occurred thousands of years ago (Laming 1959, p. 27). The behavior of bulls attacking during the rut, or when approached too closely in a defensive grouping, has not changed, and people still record these incidents, only now in the form of writing.

Ovis ?dalli (Dall sheep)

Mountain sheep remains are not uncommon in Pleistocene deposits in the Dawson Area. The only specimens collected outside of that area are from Thistle Creek, Ogilvie River and the Sixtymile Area - all within the same region. Ten cranial fragments, three maxillae with teeth (one from Alaska), and a mandible with teeth and several limb bones are described (Figure 91A-D, Tables 104-106).

Referred specimens

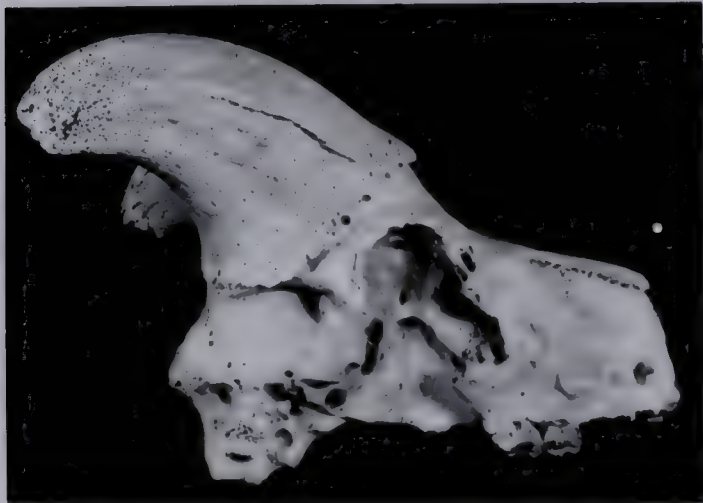
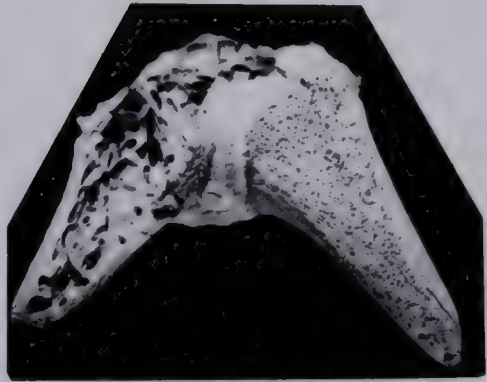
NMC 26001 from Dawson Locality 10 is the most complete cranium collected from the Dawson Area. All cheek teeth are present except for RP^2 - RP^3 and LP^3 - LP^4 . The teeth are very heavily worn, as indicated by the removal of the inner enamel patterns on the premolars. Most of the bone anterior to the P^2 s is lacking, including the anterior tips of the nasals. The right

Figure 91. Cranial fragment with horncores lacking tips (NMC 26001, Dawson Locality 10) of a Pleistocene Dall sheep (*Ovis ?dalli*) (left) and a posterior cranial fragment with a nearly complete right and a badly damaged left horncore (NMC 11371, Dawson Locality 2) of a Pleistocene Dall sheep (*Ovis ?dalli*) (right).

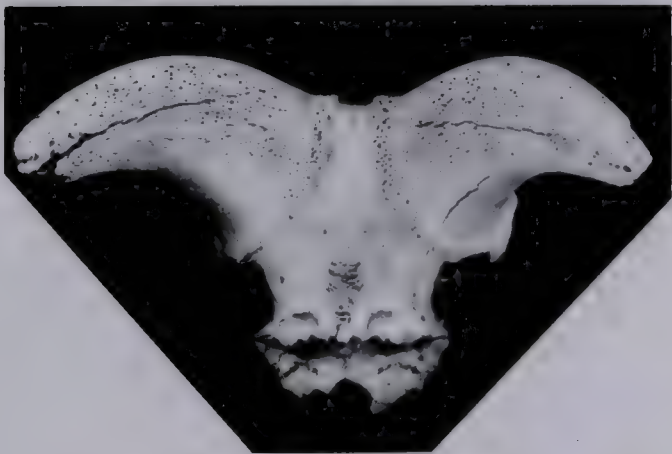
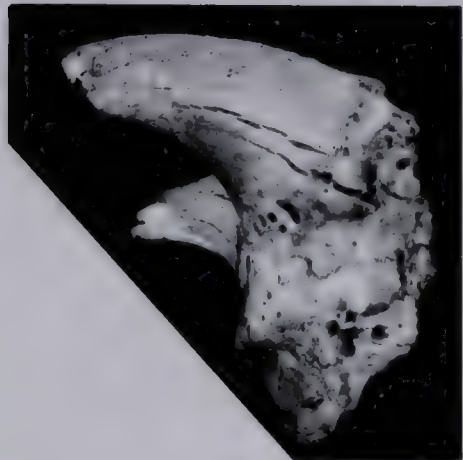
- A. Dorsal view.
- B. Right lateral view.
- C. Posterior view.
- D. Ventral view.



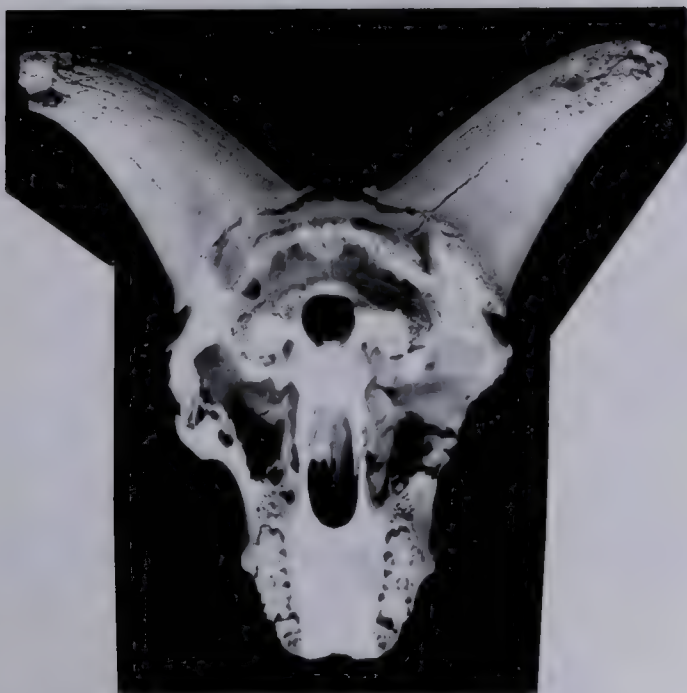
A
5 CM



B
5 CM



C
5 CM



D
5 CM

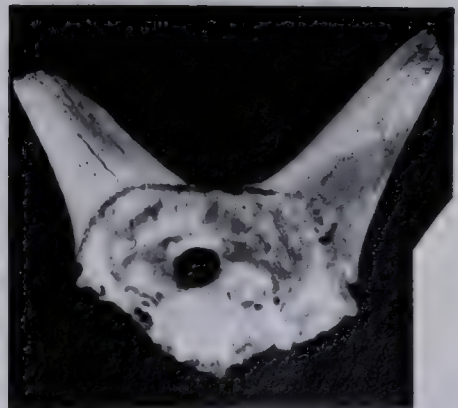


Table 104. Measurements of Pleistocene mountain sheep (*Ovis Zdalli*) crania from the Yukon Territory compared to those of Recent *Ovis dalli* and *Ovis canadensis* from North America.

Specimens	Measurements (mm)*														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Ovis Zdalli</i> . Pleistocene, Y.T.															
<u>Males</u>															
NMC 26001 Dawson Loc. 10	56.2	94.4	56.9	36.4	85.8	97.9	32.2	157.3	88.5	325.0	111.0	98.0	330.0a	228.0	70.0a
NMC 17387 Thistle Loc. 1	-	-	-	-	-	-	30.4	153.9	87.1	296.0	104.0	83.7	-	-	63.6a
NMC 7747 Dawson Loc. 9	-	-	-	-	-	-	32.4	151.8	87.8	298.0	101.3	87.8	-	-	-
NMC 11372 Dawson Loc. 2	-	-	-	-	-	-	-	139.9	84.8a	295.0	102.4	80.5	-	200.0 ⁺	-
NMC 11371 Dawson Loc. 2	-	-	-	-	-	-	30.0	142.6	86.1	285.0	100.7	78.8	-	175.0a	71.2a
NMC 11374 Dawson Loc. 2	-	-	-	-	-	-	-	-	-	243.0	84.7	65.5	-	168.0	-
NMC 17705 Ogilvie Loc. 1	-	-	-	-	-	-	27.0	132.7	81.6	255.0	88.7	70.1	-	160.0 ⁺	-
NMC 11373 Dawson Loc. 2	-	-	-	-	-	-	-	133.9	79.0a	248.0	87.0	66.0	210.0	166.0	-
Uncataloged specimen in personal collection of K. Djukastein															
Brewer Loc. 1	-	-	-	-	-	-	-	-	-	-	90.2	68.5	-	-	-
<u>Female</u>															
NMC 17411 Thistle Loc. 1	-	-	-	-	-	-	-	110.3	87.2a	114.0	41.6	32.2	93.0	50.0a	-
<i>Ovis dalli dalli</i> , Recent, N. America															
<u>Males</u> (Cowan 1940, Table 5)															
M	44.0	83.0	52.0	34.0	76.0	87.0	-	-	-	-	-	-	-	-	-
OR	38.0-	75.0-	48.0-	28.0-	72.0-	81.0-	-	-	-	-	-	-	-	-	-
	46.0	90.0	56.0	36.0	82.0	97.0	-	-	-	-	-	-	-	-	-
N	7	17	17	18	17	18	-	-	-	-	-	-	-	-	-
<u>Females</u>															
NMC 1827	-	-	-	-	-	-	-	-	78.1	-	31.8	27.6	-	59.1	-
NMC 36138	-	-	-	-	-	-	-	-	83.4	-	37.6	27.4	-	53.6	-
NMC 1850	-	-	-	-	-	-	-	-	83.3	-	36.3	26.7	-	71.0	-
NMC 17657	-	-	-	-	-	-	-	-	87.7	-	36.4a	29.2a	-	-	-
<i>Ovis canadensis californiana</i> , Recent, N. America															
<u>Males</u> (Cowan 1940, Table 19)															
M	55.0	95.0	55.0	33.0	88.0	90.0	-	-	-	-	-	-	-	-	-
OR	49.0-	86.0-	53.0-	29.0-	80.0-	81.0-	-	-	-	-	-	-	-	-	-
	61.0	101.0	59.0	38.0	95.0	93.0	-	-	-	-	-	-	-	-	-
N	5	6	6	6	6	3	-	-	-	-	-	-	-	-	-
<i>Ovis canadensis</i> , Recent, N. America															
<u>Females</u>															
NMC 8784	-	-	-	-	-	-	-	-	89.0	-	37.8	25.5	-	66.0	-
NMC 36281	-	-	-	-	-	-	-	-	90.0	-	36.3a	28.2a	-	-	-

- * 1 - Greatest width across nasals.
 2 - Minimum width across rostrum behind maxillary protruberances.
 3 - Maximum width of palate between re-entrant notches on lingual sides of M³.
 4 - Minimum width of palate between p² alveoli.
 5 - Alveolar length P²-M³.
 6 - Minimum length between M³ alveolus and anterior margin of paroccipital process on same side.
 7 - Minimum basioccipital width (between foramina ovale).
 8 - Width of cranial constriction between horncores and orbits.
 9 - Width of cranium at constriction above nuchal crest.
 10 - Circumference of horncore at burr.
 11 - Maximum anteroposterior diameter of horncore at burr.
 12 - Mediobasilar diameter of horncore at burr.
 13 - Horncore spread (tip to tip).
 14 - Horncore length from burr to tip along middle of outer curve.
 15 - Minimum width across occipital condyles.

Table 105. Measurements of Pleistocene mountain sheep (*Ovis ?dalli*) maxillae and a mandible from the Yukon Territory and Alaska compared to those of Recent *Ovis dalli* from western Canada.

Specimens	Sex	Measurements (mm)*												
		1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Ovis ?dalli.</i>														
Pleistocene, Y.T., Alaska														
<u>Maxillae</u>														
NMC 29034 Dawson Loc. 10	-	6.7	7.0	9.4	9.4	10.6	10.0	17.7	13.5	20.2	13.5	20.6	12.3	84.8
NMC 29035 Dawson Loc. 10	-	8.0	7.3	9.9	8.3	10.4	9.4	17.2	12.5	20.0	12.8	19.8	10.8	84.8
NMC 26001 Dawson Loc. 10	♂	8.9	8.4	-	-	9.3	11.5	14.2	14.8	18.4	15.5	24.4	15.7	85.8
F:AM 34656 Upper Cleary Ck., Alaska	-	7.6	7.0	8.8	8.1	10.0	9.6	14.8	12.3	17.9	12.5	20.8	11.8	76.0
<u>Mandible</u>														
NMC 17703 Ogilvie Loc. 1	-	-	-	8.2	7.0	11.1	8.3	12.9	9.2	19.0	10.8	30.2	10.4	90.6
<i>Ovis dalli.</i>														
Recent, N.W.T., B.C.														
<u>Maxillae</u>														
NMC 29850 Dal L.	♂	6.5	5.0	5.9	7.4	7.6	9.6	14.6	12.7	17.7	13.1	21.2	11.4	69.9
NMC 1849 Teslin L. area	♀	-	-	8.0	9.0	8.9	9.8	15.3	12.8	20.0	14.0	20.0	13.0	77.5
<u>Mandible</u>														
NMC 1849 Teslin L. area	♀	-	-	7.1	5.9	8.7	7.6	13.2	8.9	19.6	9.9	25.0	9.3	80.5

* 1 - P2 length.
 2 - P2 width.
 3 - P3 length.
 4 - P3 width.
 5 - P4 length.
 6 - P4 width.
 7 - M1 length.
 8 - M1 width.
 9 - M2 length.
 10 - M2 width.
 11 - M3 length.
 12 - M3 width.
 13 - P2-M3 alveolar length.

Table 106. Measurements of Pleistocene mountain sheep (*Ovis ?dalli*) metapodials from the Yukon Territory compared to those of Recent *Ovis dalli* and *Ovis canadensis* from North America.

Specimens	Sex	Measurements (mm)*						
		1	2	3	4	5	6	7
<i>Ovis ?dalli</i> .Pleistocene, Y.T.								
<u>Metacarpals</u>								
NMC 29052 Dawson Loc. 10	-	202.6	38.4	25.7	23.3	18.6	41.0	25.8
NMC 7759 Dawson Loc. 9	-	200.8	36.8	25.6	23.2	17.7	39.1	24.8
NMC 29181 Sixtymile Loc. 3	-	205.2	34.1	23.8a	23.1	17.2	37.1	24.2
NMC 29053 Dawson Loc. 10	-	187.6	32.8	21.7	19.4	15.2	33.6	21.5
NMC 10457 Dawson Loc. 12	-	-	-	-	23.9	17.7	38.0	23.8
<u>Metatarsals</u>								
NMC 29015 Dawson Loc. 16	-	225.5	29.6	29.0	19.2	20.8	36.2	24.0
NMC 29182 Sixtymile Loc. 3	-	-	30.9	28.1	18.6	18.5	-	-
<u>Metacarpals</u>								
<i>Ovis dalli</i> .Recent, N. America								
NMC 30625 N.W.T.	♂	184.2	29.7	21.6	18.0	13.9	33.4	21.8
<i>Ovis canadensis</i> .Recent, B.C.								
NMC 13753 China Head Mt.	♂	192.0	33.4	24.2	21.5	16.7	37.0	23.0
NMC 13756 B.C.	♀	181.0	29.8	21.1	18.1	13.6	32.2	21.3
<u>Metatarsals</u>								
<i>Ovis dalli</i> .Recent, N. America								
NMC 30625 N.W.T.	♂	200.1	26.0	25.5	16.2	15.2	31.9	22.2
<i>Ovis canadensis</i> .Recent, B.C.								
NMC 13753 China Head Mt.	♂	211.0	29.6	27.4	18.7	18.9	34.0	24.2
NMC 13756 B.C.	♀	200.9	26.8	25.7	16.1	16.0	31.0	22.1

- * 1 - Total length.
 2 - Proximal width.
 3 - Proximal depth.
 4 - Midshaft width.
 5 - Midshaft depth.
 6 - Distal width.
 7 - Distal depth.

horncore is slightly abraded at the tip, and approximately 30 mm is missing from the end of the left horncore. Most of the right malar and the inferior part of the right supraorbital process are lacking, leaving only the upper rim of the right orbit intact. The rim of the left orbit and the margins of the occipital region are eroded. The zygomatic arches are broken. The large size of the horncores, the heavy tooth wear and the fusion of both frontal and frontonasal sutures indicate that NMC 26001 represents an old male. The cranium is larger in six important measurements than the largest Dall sheep (*Ovis dalli dalli*) crania sampled by Cowan (1940, Table 5), and is close to the means of the same measurements that he took on several bighorn sheep (*Ovis canadensis californiana*) (Table 104). Because I am not aware of any qualitative means of differentiating Dall from bighorn sheep on the basis of cranial characters, I see no reason why the specimen could not be identified as *Ovis canadensis*. However, when the great variation in body size, and horn size and shape, of mountain sheep due to different levels of nutrition and population density (Shackleton 1973) are considered, and the present dispersal patterns of southern and northern mountain sheep are taken into account (evidently bighorn sheep and Dall sheep have not met in the Peace River region during postglacial time), it seems most likely that NMC 26001 represents a late Wisconsin

large phase (chronosubspecies?) of mountain sheep presently known as *Ovis dalli stonei*. The same explanation may apply to other specimens in the collection, such as the unusually large metapodials. The light tan color and fresh appearance of NMC 26001 suggest it is of late Wisconsin age.

NMC 17387 from Thistle Locality 1 was collected in 1901 by R.G. McConnell. It consists of the posterior part of a cranium with horncores. The distal half of the right horncore and the distal third of the left horncore are missing. Most of the bone anterior to the orbits is lacking. The upper parts of the orbits are preserved, but their rims are heavily worn. The lateral margins of the occipital region, and the occipital condyles are heavily worn also. The large horncores and fused frontals indicate that this specimen represents an adult male. NMC 17387 has the fresh appearance of NMC 26001, and is probably of late Wisconsin age.

NMC 7747 from Dawson Locality 9 was collected by D.D. Cairnes in 1911. It consists of a badly damaged posterior cranial fragment. Micaceous sandy silt in the pneumatic cavities of the cranium suggests that the fossil was derived from muck deposits. The distal halves of the

horncores, and bone anterior to the horncore bases are lacking. Both occipital and basioccipital regions are heavily eroded. The large size of the horncores, the obliteration of the frontal suture, and the exostoses along the midline above the nuchal crest indicate that NMC 7747 represents an old male. The fragment is tan to light buff and may be of late Wisconsin age.

NMC 11372 from Dawson Locality 2 is a posterior cranial fragment lacking the occipital and basioccipital regions and bone anterior to the horncore bases. Most of the left horncore is preserved, while only the proximal third of the right horncore is present. The fossil has weathered to a light buff color, except for the oxidized posteromedial surface of the left horncore. The size of the horncore and obliteration of the frontal suture indicate that the specimen represents an old male.

NMC 11371 from Dawson Locality 2 is a posterior cranial fragment lacking bone anterior to the horncore bases and the anterior half of the left horncore. The tip of the right horncore is missing. The large size of the horncores and the fusion of the frontal suture indicate that the fossil represents an adult male. NMC 11371 is

dark tan.

NMC 11374 from Dawson Locality 2 is part of the right side of a posterior cranial fragment. In addition to a virtually complete right horncore, the upper portion of the right orbit and segments of the right frontal (attached to part of the left frontal), parietal, temporal and squamosal are preserved. The frontal suture is open, except for a small area at the level of the orbits. The large size of the horncore and the low degree of fusion of the frontal suture indicate that the specimen represents a male in early adulthood. It is dark tan.

NMC 17705 from Ogilvie Locality 1 is a posterior cranial fragment that lacks bone anterior to the horncores. All but the tip of the right horncore is preserved, while most of the left horncore and the left frontal are missing. The borders of the occipital and basioccipital regions are heavily eroded. Only the lateral parts of the frontoparietal suture are fused. The small degree of fusion and the relatively large size of the horncore indicate that NMC 17705 represents a male in early adulthood. The surface of the specimen is heavily weathered, and is dark tan.

NMC 11373 from Dawson Locality 2 consists of both horncores and surrounding frontal and parietal bones. The tips of the horncores are slightly abraded. Frontal sutures are open. The condition of the sutures and the relatively large horncores indicate that NMC 11373 was derived from a male in early adulthood. The posterior surface of the fossil is heavily iron-stained.

NMC 29189 from Sixtymile Locality 3 is a fragment comprising the anterior part of the frontals and horn-core bases. Frontal sutures are fused, and the parts of the horncores preserved are massive, suggesting that the specimen represents a large, adult male like NMC 17387. The bone is pale and fresh in appearance. The specimen may be of late Wisconsin age. No useful measurements can be taken on it.

NMC 17411 from Thistle Locality 1 was collected at Edas Gulch in 1901 by R.G. McConnell. It consists of fused frontals and attached, complete horncores. On the basis of its small horncores with their tendency to lateral compression and the obliteration of the frontal suture, I refer it to an old female. NMC 17411 is slightly larger in most measurements than the same region of six female *Ovis dalli* crania and two female

Ovis canadensis crania to which it was compared.

Possibly McConnell's (1905) report of mountain goat (*Oreamnos americana*) remains from Pleistocene gravels in the Klondike district may be explained by this specimen. Its original label reads: "10. Horncores with frontal. Antelope ?? From Edas Gulch, Thistle Cr., Y.T. Collected by R.G. McConnell, 1901." This fossil with its small, straight horncores could easily be mistaken for a mountain goat. The significant points of difference between NMC 17411 and *Oreamnos* are the greater breadth of the cranium of NMC 17411 (including the distance between horncores - approximately 46 mm), and the pronounced lateral compression of the horncores of NMC 17411 compared to their roundness in *Oreamnos*. Only two other specimens collected by McConnell are in the collection: a cranial fragment of an adult male *Ovis ?dalli* (NMC 17387 - mentioned previously) from Thistle Creek; and a partial cranium of *Bison crassicornis* (NMC 7392) from Gold Run Creek. Neither could be mistaken for a mountain goat fossil. If McConnell's report of Pleistocene mountain goat remains were not based on the erroneous identification of NMC 17411, it would still have to be dismissed for lack of solid evidence (Harington 1971b, p. 1093).

In 1967, K. Djukastein loaned me a braincase with horncores (tips missing) of a mountain sheep that he had collected from Pleistocene deposits at Brewer Locality 1. It was slightly larger in basal horncore dimensions than a Recent specimen of similar age of *Ovis dalli* (NMC 15387), but was closer to it than a Recent cranium of *Ovis canadensis*, with which it was compared at the same time. I have not examined a posterior cranial fragment with horncores (ROM 5304) of a mountain sheep collected by a Dr. Burwash from Pleistocene deposits at an unspecified locality in the Yukon Territory.

In the collections are two well preserved maxillae with teeth. NMC 29034 from Dawson Locality 10 is a left maxilla with LP^2-LM^3 . It has the size, tooth pattern, and facial tuberosity above M^1 that characterize mountain sheep. The shape of the malar-maxillary suture is of diagnostic importance in separating mountain sheep from mountain goats (*Oreamnos*), goats (*Capra*) and the North American prongbuck "antelopes" (e.g. *Antilocapra*, *Tetrameryx*). The maturely worn teeth and the well developed protruberance above M^1 suggest that NMC 29034 represents an adult. NMC 29035 from Dawson Locality 10 is a right maxilla with RP^2-RM^3 . It is similar to NMC 29034 and has the same tan color, but there is no

evidence that they fit together. The posterior cusp of RM^3 is less heavily worn than that of NMC 29034.

For comparative purposes, a right maxilla with teeth (F:AM 34656) from Upper Cleary Creek in the Fairbanks area, Alaska is described. I am grateful to R.H. Tedford of the Frick Laboratory, American Museum of Natural History for the loan of this specimen. Unlike the other two fossils, it has most of the malar bone. Its P^2-M^3 alveolar length is approximately 10% shorter than those of the Yukon fossils, but almost the same as that of a Recent female of *Ovis dalli* (NMC 1849), which may indicate that smaller mountain sheep (*Ovis dalli dalli* progenitors?) lived in central Alaska, while larger ones (*Ovis dalli stonei* progenitors?) lived in the southeastern extremity of the Eastern Beringian refugium during the late Wisconsin. Detailed comparison of Fairbanks area mountain sheep fossils, and those from the Dawson Area are required in order to test this hypothesis.

NMC 17703 from Ogilvie Locality 1 is part of a left mandible with LP_3-LM_3 , the alveolus for LP_2 , and most of the diastema. The inferior border of the jaw from below LP_4 to below LM_3 is lacking. The occlusal

surfaces of the teeth are moderately worn, indicating that an adult is represented. The fossil is dark tan and has a weathered, finely-cracked surface.

Several mountain sheep limb bones are in the Yukon collections. USDG 11 from Sulphur Creek in the Dawson Area is the left humerus of a subadult. It is complete except for the proximal epiphysis, which evidently was not fused to the shaft. The animal may have been between approximately 3 to 3.5 years old when it died, according to the age when this epiphysis fuses to the shaft in domestic sheep (*Ovis aries*). In morphological details, USDG 11 matches a humerus of a slightly older Recent male of *Ovis dalli* (NMC 30625) from the Yukon, but it is about 23% shorter. The fossil is stained dark reddish brown and may be older than late Wisconsin. W.G.E. Caldwell kindly allowed me to borrow this specimen from the University of Saskatchewan, Department of Geology collection.

NMC 11375 from Dawson Locality 2 is a fragment of a right radio-ulna. The proximal half of the radius, and the proximal third of the ulna (near the semilunar notch, lacking the olecranon) are preserved. The maximum proximal width of NMC 11375 is 40.3 mm compared

to 41.0 mm for the same measurement in a Recent *Ovis dalli* radio-ulna (NMC 30625). The fossil is light tan and very fresh looking. I suggest it is of late Wisconsin age.

The metapodials are interesting in that they give a good idea of the size of the late Pleistocene mountain sheep in the Dawson region of the Yukon Territory. Evidently all are from mature individuals, for the distal epiphyses are fused to the shafts, and the tuberosities on their anterior surfaces near the proximal ends are well developed. Four of the metacarpals and both metatarsals are probably from animals the size of Recent male bighorn sheep (*Ovis canadensis*), while only one metacarpal corresponds in size to metacarpals of Recent Dall sheep (*Ovis dalli*).

NMC 29052 from Dawson Locality 10 is a complete right metacarpal. It is larger than a Recent adult male bighorn sheep metacarpal (NMC 13753), and approximately 9% longer than a modern *Ovis dalli* metacarpal (NMC 30625). NMC 10457 from Dawson Locality 12, the distal half of a right metacarpal, is comparably large. NMC 29053 from Dawson Locality 10 is a complete right metacarpal that is similar in size to a metacarpal of a Recent

male of *Ovis dalli* (NMC 30625), and a Recent female of *Ovis canadensis* (NMC 13756). Pyrolusite "stars" decorate the shaft. The fact that both large (NMC 29052) and small (NMC 29053) metacarpals were collected from the same muck deposit, at the same locality, in the same year, and that, according to their fresh appearance both are probably of late Wisconsin age, suggests that the former represents a male and the latter a female of the same species. Northern Dall sheep (*Ovis dalli dalli*) males are now about 30% heavier than females of that subspecies (Banfield 1974, p. 417), which could explain the size differences between the fossils. More comparative material is required to obtain a clear picture of the variations in limb bone size between males and females of Recent mountain sheep.

NMC 7759 from Dawson Locality 9 is a large left metacarpal. A patch of bone is missing on the posterior surface of the shaft just above the distal articulation. A small projection of bone on the posterolateral margin near the middle of the shaft suggests that NMC 7759 was derived from an old individual. The dark brown surface staining is due to a covering of dark preservative. NMC 29181 from Sixtymile Locality 3, another left metacarpal, is longer than NMC 7759, and

is damaged on the posterior edge of the proximal articulation. The posterior surface of the shaft is weathered, cracked and oxidized.

Two metatarsals are in the collection. NMC 29015 from Dawson Locality 16 is complete, and very fresh looking. It is approximately 11% longer than Recent *Ovis dalli* metatarsals with which it was compared - one of which (NMC 30625) is from a male - and is 6% longer than the metatarsal of a male bighorn sheep (NMC 13753). NMC 29182 from Sixtymile Locality 3 lacks the extremities, but seems to have been similar in size to NMC 29015. Modern northern Dall sheep (*Ovis dalli dalli*) males are approximately 6% longer in the hindfoot than females of that subspecies (Banfield 1974, p. 417), which provides an idea of the large size of some of the late Wisconsin mountain sheep. A single first phalanx (NMC 29033) from Dawson Locality 10 is 62.1 mm in total length. It was collected *in situ* from muck approximately 1 foot (0.3 m) above bedrock.

Discussion

So far, mountain sheep fossils from the Yukon Territory have been collected only in the Dawson region (Dawson Area, Sixtymile Area, and Thistle and Ogilvie localities). Evidently the margins of the Old Crow Basin were relatively poor mountain sheep range during the late Pleistocene. With one or two exceptions, all of the specimens are pale tan and fresh in

appearance, suggestive of a late Wisconsin age. Bone from a horncore of *Ovis dalli* from Dawson Locality 2 yielded a radiocarbon date of $23,000 \pm 600$ years B.P. (I-4225), which supports the contention that mountain sheep occupied Eastern Beringia during the late Wisconsin glaciation. My impression is that the fossils are unusually large - more the size of modern *Ovis canadensis* than of *Ovis dalli* - although zoogeographically it is more probable that they represent Dall sheep, which, like *Ovis canadensis catclawensis* in the southern refugium (Harris and Mundel 1974, p. 679), attained great body size during the late Wisconsin.

The earliest mountain sheep ("*Ovis canadensis*") remains in Canada are from Sangamon interglacial deposits at Medicine Hat, Alberta (Stalker and Churcher 1971). A fragmentary metacarpal of *Ovis canadensis* from gravels at Cochrane, Alberta appears to be larger than a Recent metacarpal of *Ovis canadensis* to which it was compared. Radiocarbon analyses of *Bison bison occidentalis* bone from the same deposit at Cochrane gave dates of approximately 11,000 years B.P. (Churcher 1968b, pp. 1470-1471). The only other mountain sheep fossils from Canada have been found in British Columbia. A well preserved cranium of a male bighorn sheep (*Ovis canadensis*)

was collected from a gravel pit near Finlay Forks. Bone from a horncore yielded a radiocarbon date of $9,280 \pm 200$ years B.P. (GSC-1497) (Rutter *et al.* 1972, p. 641).

Several partial crania of *Ovis canadensis* were recovered from the bed of Tranquille Creek and adjacent Hanging Valley Creek in southern British Columbia. Cowan (1941, p. 47) considered them to be of Pleistocene or early postglacial age.

In the conterminous United States, *Ovis canadensis* remains have been identified from many localities in the west, such as: Jaguar Cave, Idaho; Little Box Elder Cave, Wyoming; Dry Cave, Isleta Caves and Burnet Cave, New Mexico; Gypsum Cave, Catclaw Cave, and Winnemucca, Nevada; Rampart Cave and Stanton Cave, Arizona; Glendale, California; and near Lake Bonneville, Utah. Most of the specimens are from deposits of Wisconsin age. Fossils from the Great Basin once assigned to "*Ovis catclawensis*", and now perhaps best considered as representing a large chronosubspecies of the bighorn sheep, *Ovis canadensis catclawensis*, are probably of early to mid-Wisconsin age (approximately 68,000 to 33,000 years B.P.) (Stock and Stokes 1969, p. 805). Organic material associated with remains of very large sheep comparable to "*Ovis catclawensis*" in Dry Cave, New Mexico yielded a radiocarbon date of

15,030 \pm 210 years B.P. (I-6201). A specimen identified as modern *Ovis canadensis* from near Winnemucca, Nevada was considered to be about 6,500 years old by Stokes and Condie (1961).

The earliest records of mountain sheep in North America are from Alaska. "*Ovis* sp." has been identified from loess considered to be of Illinoian age by T.L. Péwé at Cripple Creek sump near Fairbanks (Péwé and Hopkins 1967, pp. 268-269). A metatarsal probably referable to mountain sheep ("cf. *Ovis* sp.") was collected from outwash sediments of Illinoian age in the Nenana Valley near Fairbanks (Péwé and Hopkins 1967, pp. 268-269). Most mountain sheep specimens, including several good crania, have been collected from the Fairbanks area (e.g. Fairbanks Creek, Engineer Creek, Cripple Creek, and Gold Hill) (Frick 1937, p. 555; Guthrie 1968b, Table 1). I have identified mountain sheep remains from late Wisconsin deposits at Lost Chicken Creek in eastern Alaska (Harrington 1976 MS., p. 78) and from deposits of late Pleistocene age at Canyon Creek in the Big Delta area. Two specimens were derived from stream channel fill at the latter site. The distal half of a left metatarsal was comparable in size to the same part of a Recent female of *Ovis canadensis* (NMC 32243). A partial RM³

was found to be slightly longer anteroposteriorly than RM^3_s of *Ovis dalli* (NMC 29850, 1849). I am grateful to C.A. Repenning of the U.S. Geological Survey for sending these fossils for examination. Material identified as "Hypsodont bovid (sheep or goat)" from the Sullivan Pit near Tofty (Repenning *et al.* 1964, Table 1) probably pertains to mountain sheep.

Ovis fossils have not been recorded from any of the major northeastern Siberian Pleistocene vertebrate faunas, presumably because their lowland situations were not favorable for mountain sheep during the Pleistocene. However, *Ovis* specimens are known from late Pleistocene deposits of south central Siberia (near Krasnoyarsk and Irkutsk), Transbaikalia and central Asia. In China, *Ovis* has been recorded from upper Pliocene sediments (Gromova 1968, p. 544).

Farther west, in the Caucasus remains of large sheep of the argali type ("*Ovis* cf. *ammon*") are very rare, and have been found only in middle and upper Pleistocene deposits of the Transcaucasian mountains and plains. Fossils of the Asiatic mouflon, "*Ovis gmelini*" (*Ovis orientalis gmelini*), are rarer, having been collected only from Paleolithic deposits of the Lesser Caucasus

and the Mesolithic of Dagestan (Vereshchagin 1959, p. 370).

In Europe, the earliest remains of *Ovis* occur in Villafranchian deposits (e.g. Senèze in southern France). *Ovis* fossils of middle Pleistocene age are known from Pont-du-Chateau in France and from the Cromer Forest Bed at Overstrand, England. During the late Pleistocene, the European mouflon (*Ovis musimon*) seems to have been fairly common in Italy and North Africa (Kurtén 1968, p. 180).

Ovis may have arisen from goat-antelope (Rupicaprinae) ancestors in mountainous country of Asia, whence, toward the close of the Pliocene, sheep spread rapidly eastward to China and westward toward southern Europe (Senèze). The urial sheep (*Ovis vignei*) of central Asia (northeastern Iran to Tadzhikistan and Afghanistan — a region that did not undergo severe glacial and climatic changes during the Pleistocene) are probably the most primitive. Cytogenetic data seem to throw a great deal of light on the pattern of evolution of *Ovis*. The urials of central Asia have the highest chromosome complement of 58. West of the urial range (Mediterranean to Iran), the Asiatic mouflon (*Ovis orientalis*) and

European mouflon (*Ovis musimon*) have 54 chromosomes, whereas east of the urial range (Pamirs, Tien Shan, and Altai mountains through Tibet and Mongolia to China), the argali or arkhar (*Ovis ammon*) has 56 chromosomes (Nadler *et al.* 1973, pp. 115-116). Still farther east, are the western Beringian snow sheep (*Ovis nivicola*) with a complement of 52 chromosomes. In western North America are Dall sheep (*Ovis dalli*) and bighorn sheep (*Ovis canadensis*) with 54 chromosomes (Korobitsyna *et al.* 1974, p. 235). Presumably the ancestral mountain sheep of Beringia that gave rise to American Dall and bighorn sheep and Siberian snow sheep had a chromosome complement of 54. The *Ovis nivicola* karyotype of $2n = 52$ may have evolved from the $2n = 54$ condition since the flooding of the Bering Isthmus about 12,000 years ago (Korobitsyna *et al.* 1974, p. 242), or, in my opinion, earlier. Robertsonian centric fusion appears to be the key cytological event responsible for creating this remarkable set of "prints", which seems to lead from the late Pleistocene of Beringia back to the late Pliocene of central Asia. Nadler *et al.* (1973, p. 116) state: "Considerable direct and indirect evidence suggests that fusion rather than fission is the predominant mechanism for changes in diploid number in cattle, sheep and goats, and it seems probable that the $2n = 58$ or urial sheep is the most representative of the ancestral sheep chromosome complement and that the sheep with $2n = 56$ and $2n = 54$ karyotypes evolved from the former."

Mountain sheep of North America were derived from a western Beringian stock that first entered Eastern Beringia (Fairbanks) via the Bering Isthmus during the Illinoian glaciation. The flooding of the Bering Isthmus at the beginning of the Sangamon interglacial established a break between the ancestors of the snow and Dall sheep. Contact between these sheep may not have been renewed during the succeeding Wisconsin glaciation, allowing more time than Korobitsyna *et al.* (1974, p. 242) have suggested for chromosomal divergence of the snow sheep. During the Sangamon interglacial, the stock (which I postulate looked like Stone sheep (*Ovis dalli stonei*)) that gave rise to bighorn sheep had reached west-central North America (Medicine Hat). Like the first bison entering the region, favorable range and competitive advantage seem to have resulted in the development of very large animals with massive horns toward the close of the Sangamon interglacial (e.g. *Ovis canadensis catclawensis* in the Great Basin).

Harris and Mundel (1974, p. 679) postulate that sheep populations with relatively large-sized males were widespread in the western United States and northern Mexico during the late Wisconsin, and that there was a selection for smaller size at the close of the Wisconsin

as a result of environmental deterioration. Further, they suggest that the smaller, modern bighorn subspecies were derived from *Ovis canadensis catclawensis* about 10,000 years ago. Therefore, it may be possible to use remains of extremely large male mountain sheep in the southern refugium as index fossils of "pre-postglacial" deposits. Thus, the larger, darker southern mountain sheep were isolated from their paler, ancestral brothers in the north during the Wisconsin glaciation.

Among the mountain sheep isolated in Eastern Beringia (Dawson region) were some that corresponded in size to modern *Ovis canadensis*. I speculate that those sheep occurring in the southeastern portion of Eastern Beringia during the late Wisconsin were derived from populations that had occupied the mountains of northern British Columbia during the Sangamon interglacial, and that had characteristics lying between northern Dall sheep and southern bighorn sheep (e.g. larger size and darker pelage). I postulate: (a) that as Cordilleran ice expanded, the northern British Columbian sheep were forced northward into the southern Yukon near the peak of the Wisconsin glaciation about 20,000 years ago; (b) that they were largely separated from smaller, paler *Ovis dalli dalli*, which may have been concentrated in central Alaska; and (c) that they may be identified as progenitors of the modern Stone sheep

(*Ovis dalli stonei*). As the Wisconsin ice melted back, these sheep again moved southward, while *Ovis dalli dalli* spread toward their range, some intergradation occurring near the present Yukon - British Columbia border. This hypothesis combines elements of two others. The first, advocated by Geist (1971), is that Stone sheep survived the Wisconsin glaciation in the Alaska - Yukon refugium; and the second, put forward by Youngman (1975, p. 174), is that Stone sheep were "a southern {relative to Eastern Beringia} Rocky mountain isolate" (but where could they have been isolated according to our present knowledge that northern British Columbia was smothered by ice (Prest 1969)?).

I think that the nomenclature of North American mountain sheep should be altered to more accurately reflect the following factors: (a) recent cytogenetic findings of Nadler, Korobitsyna and their colleagues that all North American mountain sheep have a chromosome complement of 54, whereas Siberian snow sheep have 52; (b) the great variability in body size, size and shape of horns, and color, depending on quality of range, population density and latitude (Gloger's "rule" seems to be operating as indicated by the darkening of mountain sheep pelage at lower latitudes, where warmer, moister conditions prevail); and (c) the existence of an intermediate

variety of mountain sheep (*Ovis dalli stonei*) between Dall sheep to the north and bighorn sheep to the south.

Consequently, I suggest that the name *Ovis nivicola* be retained for the snow sheep of Siberia, and that North American mountain sheep be designated as a single, rather variable species, *Ovis canadensis* (*canadensis* has priority over *dalli*), including three subspecies:

Ovis canadensis canadensis (bighorn sheep), *Ovis canadensis stonei* (Stone sheep), and *Ovis canadensis dalli* (Dall sheep).

Dall sheep occupy mountain ranges of northwestern North America from the west coast of Alaska through most of the Yukon Territory, and part of the Northwest Territories west of the Mackenzie River, to northern British Columbia. The Ogilvie River area, where the fossil mandible NMC 17703 was collected, is one of the most productive areas of Dall sheep range in the Yukon. Stone sheep (*Ovis dalli stonei*) range from northern British Columbia (north of the Peace River) into the south-central Yukon.

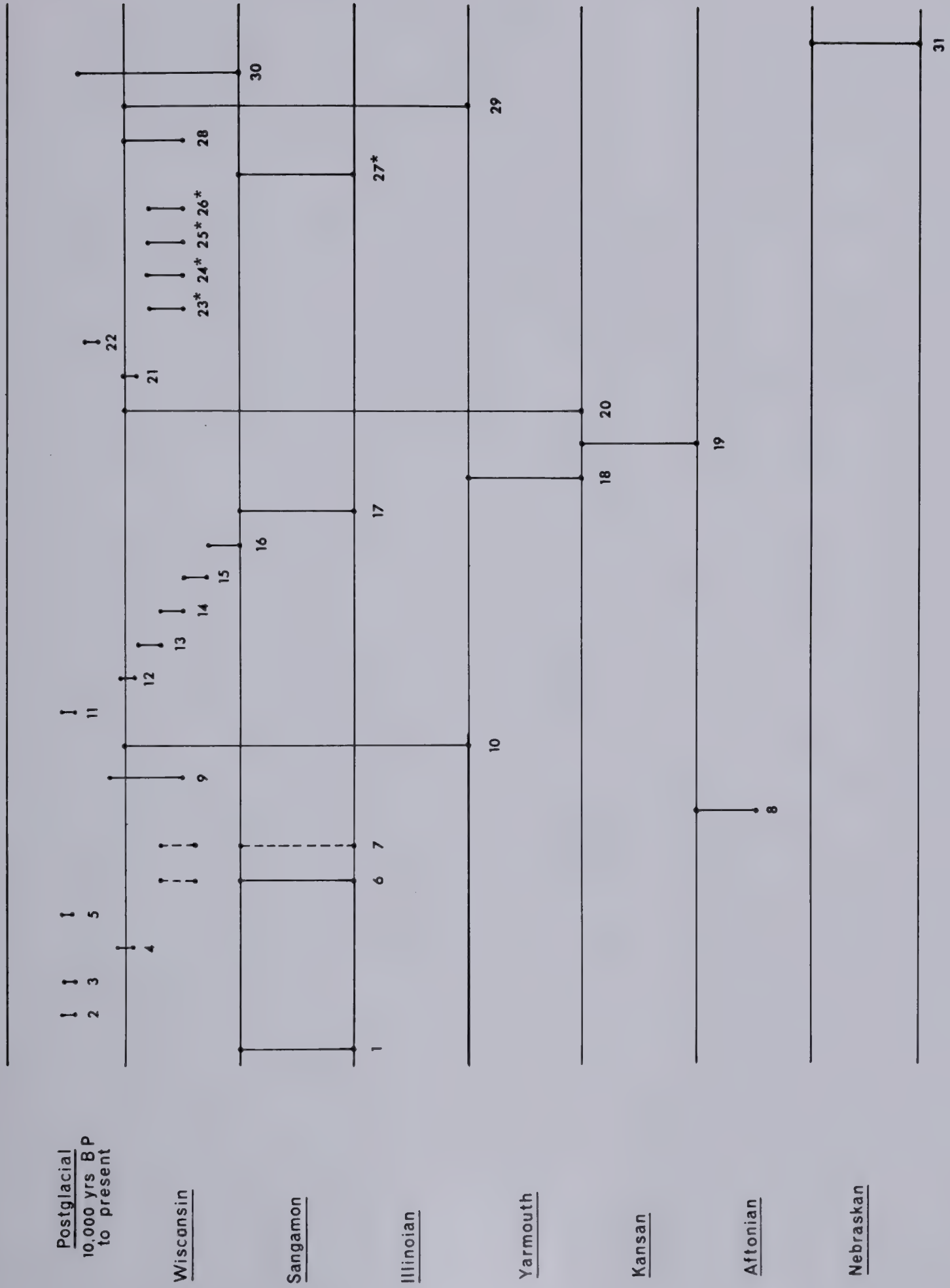
Dall sheep are smaller than bighorn sheep and have a shorter face. Their pale amber horns are more

slender than those of the bighorn, and they flare more toward the tips. There are two well-marked color phases. The northern group (*Ovis dalli dalli*) is creamy white, except for a few dark hairs along the spine and tail. The southern group (*Ovis dalli stonei*) is slate brown, except for small white patches on rump and muzzle, and varying amounts of white on the insides of the legs and on the forehead. Intergrades between the two groups are sometimes mainly white with dark "saddles". The winter coat of Dall sheep is long, providing good insulation against the cold. Dall sheep are gregarious, forming bands led by old females, which usually comprise 10 animals, but often include more during the winter, when the rams join them. In autumn, during the rut, the males have butting duels, much like tundra muskoxen. They are superb climbers. Their hooves, with spongy centres and hard rims, ensure a firm grip on rock. They have keen senses of vision and smell.

In summer, Dall sheep males separate from the bands of females and lambs. All move to preferred habitat in high (up to elevations of 6,000 feet (1,829 m)) alpine pastures. In September or early October the groups descend to lower, drier, south-facing slopes. Their numbers may be greatly reduced by heavier than

average snowfalls. Grasses and sedges are the main diet . of Dall sheep. During the summer they feed on saxifrages, locoweed, licorice root, and horsetails. In winter they paw snow away to feed on woody plants such as willow, sage, cranberry, crowberry and mountain avens. Predation by wolves is most critical during the migration period, when bands may have to cross open tundra to reach winter range. Perhaps it was the relative lowness and lack of good cover that prevented mountain sheep from flourishing in the Old Crow Basin during the Pleistocene, while they evidently thrived in the higher more rugged country near Dawson. Lynx, wolverines, coyotes and grizzly bears are other important predators. Golden Eagles occasionally prey on young lambs (Banfield 1974, p. 417).

Figure 92. Suggested chronological sequence of Pleistocene vertebrate faunas of Canada and Alaska. Yukon Pleistocene mammal faunas are marked with asterisks to show their relationships with the other faunas. Solid vertical lines indicate probable age, dashed ones indicate possible age. Details of each fauna are provided elsewhere (Harrington 1976 MS.) according to its number: 1. Toronto, Ontario (Don Formation); 2. Toronto, Ontario (Scarborough Bluffs); 3. Hamilton, Ontario (Hamilton Bay); 4. Ottawa, Ontario (Greens Creek); 5. Oxbow Dam, Saskatchewan; 6. Fort Qu'Appelle, Saskatchewan (Echo Lake Gravels); 7. Saskatoon area, Saskatchewan (Floral Formation); 8. Wellsch Valley, Saskatchewan; 9. Empress, Alberta; 10. Bindloss area, Alberta; 11. to 19. Medicine Hat, Alberta faunas; 20. Hand Hills, Alberta (Hand Hills Conglomerate).



21. Cochrane, Alberta (Big Hill Creek Formation); 22. Acasta Lake, Northwest Territories; 23.* Gold Run Creek, Yukon Territory (Dawson Locality 32); 24.* Hunker Creek, Yukon Territory (Dawson Locality 16); 25.* Sixtymile River, Yukon Territory (Sixtymile Locality 3); 26.* Old Crow River, Yukon Territory (Old Crow Locality 14N); 27.* Old Crow River, Yukon Territory (Old Crow Locality 44); 28. Lost Chicken Creek, Alaska; 29. Fairbanks area, Alaska; 30. Sullivan Pit, Alaska (Tofty Placer District); 31. Cape Deceit, Alaska (Cape Deceit Formation).

CONCLUSIONS

1. From 1966 to 1975, approximately 14,000 Pleistocene vertebrate fossils were collected in the Yukon Territory for the National Museums of Canada. Most came from the Old Crow Basin, which I consider to be the richest area for Pleistocene mammal fossils in Canada. Many specimens have been collected in the Dawson Area also, and most of the conclusions reached here were based on an examination of this evidence, and an attempt to interpret it. Only several hundred of the most complete, or significant fossils are described in this study.

2. Ten orders (Insectivora, Primates, Edentata, Lagomorpha, Rodentia, Cetacea, Carnivora, Proboscidea, Perissodactyla, Artiodactyla), 19 families, 44 genera and 64 species of mammals have been identified from Yukon Pleistocene deposits. Among the families, the Cricetidae, Mustelidae, Equidae and Bovidae are most strongly represented; and among the genera, *Equus* and *Bison* seem to be represented by the greatest number of species. Two of the species, a large whale and a seal, are marine mammals, while the remainder are land mammals. The number of muskox genera (four or possibly five, if *Bootherium sargenti* and *Symbos cavifrons* are not female and male of the same species) is perhaps not surprising, considering the northern latitude

of the fossil localities. It is worth noting that all stages of North American mammoths are represented in the Yukon: the southern mammoth (*Mammuthus meridionalis*), the steppe mammoth (*Mammuthus* cf. *armeniacus*) and the woolly mammoth (*Mammuthus primigenius*).

3. Horse, mammoth, bison and caribou are the commonest species of large mammals represented in the Yukon fossil collections. Muskrat, ground squirrel, brown lemming and pika remains are very common among the small mammal specimens. Most of these species are adapted to cool grassland or tundra environments.

4. The discovery of a caribou tibia fleshing tool made by man at Old Crow Locality 14N is of great interest because radiocarbon analysis of a sample of bone from it yielded a date of $27,000 \pm \begin{matrix} 3000 \\ 2000 \end{matrix}$ years B.P. It suggests that people were present in Eastern Beringia at least as early as mid-Wisconsin time. Evidence suggests that they hunted caribou, mammoth, horse and bison. The find of a caribou antler punch or wedge with Pleistocene mammal remains at Dawson Locality 16 may indicate that these early hunters were present in that region also. A deeply permineralized mandible of a domestic dog from Herschel Island is tantalizing. It may imply that people lived near the northern coast of the Yukon before the late Wisconsin

maximum. Stone bifacial tools, including "knives" and a projectile point have been found in reworked deposits in the Old Crow Basin. Their age is uncertain.

5. Approximately 40% of the mammal species known as fossils from Yukon Pleistocene deposits are extinct, and about 60% no longer occur in the Yukon. Horses (all five species are considered to be extinct), bison, elephants, camels, muskoxen and large cats were particularly reduced by extinctions.

6. Mammal fossils which appear to be characteristic of the early, middle and late Pleistocene have been found in the Yukon Territory. The plains shrew (*Planisorix* cf. *dixonensis*), the giant pika (*Ochotona* cf. *whartoni*) and the southern mammoth (*Mammuthus meridionalis*) are considered to be good indicators of the early Pleistocene. Probably Soergel's muskox (*Soergelia* cf. *elisabethae*), Staudinger's muskox (*Praeovibos priscus*), giant moose (*Alces latifrons*), steppe mammoth (*Mammuthus* cf. *armeniacus*), large horses (*Equus* cf. (*Plesippus*) *verae*), and possibly the dhole (*Cuon* sp.) and Hensel's lemming (*Dicrostonyx* cf. *henseli*) are indicative of a middle Pleistocene element. Among mammals that typify the late Pleistocene in the Yukon are the woolly mammoth (*Mammuthus primigenius*), moose (*Alces alces*), Yukon wild ass (*Equus (Asinus) lambei*), Dall sheep (*Ovis ?dalli*),

helmeted muskox (*Symbos cavifrons*), tundra muskox (*Ovibos moschatus*), arctic fox (*Alopex lagopus*), American lion (*Panthera leo atrox*), American badger (*Taxidea taxus*), large-horned bison (*Bison crassicornis*), and the western bison (*Bison bison occidentalis*) which occurred near the close of the Wisconsin glaciation.

7. Radiocarbon dates pertaining to Yukon and Alaskan Pleistocene mammal fossils help to indicate the species that were present in Eastern Beringia during Wisconsin and postglacial time. Within the limits of the radiocarbon dating technique, chronological ranges for various species follow: ground squirrel (*Spermophilus parryi*) $14,760 \pm 850$ years B.P. to $14,510 \pm 450$ years B.P.; beaver (probably *Castor canadensis*) $9,330 \pm 300$ years B.P. to $3,700 \pm 150$ years B.P.; American lion (*Panthera leo atrox*) $22,680 \pm 300$ years B.P.; woolly mammoth (*Mammuthus primigenius*) $30,300 \pm 2,000$ years B.P. to $15,380 \pm 300$ years B.P.; large horse (*Equus* sp., probably *Equus* cf. (*Plesippus*) *verae*) $>39,900$ years B.P. to $34,000 \pm 2,600$ years B.P.; Yukon wild ass (*Equus (Asinus) lambei*) probably $26,760 \pm 300$ years B.P. to $14,870 \pm 260$ years B.P.; western camel (*Camelops* sp.) $24,900 \pm \begin{smallmatrix} 1100 \\ 1000 \end{smallmatrix}$ years B.P.; wapiti (*Cervus elaphus*) $4,570 \pm 100$ years B.P.; giant moose (*Alces latifrons*) $33,800 \pm 2,000$ years B.P.; caribou (*Rangifer tarandus*) $27,000 \pm \begin{smallmatrix} 3000 \\ 2000 \end{smallmatrix}$ years B.P. to $5,010 \pm 100$ years B.P.; Alaskan bison (*Bison*

alaskensis) >39,900 years B.P.; large-horned bison (*Bison crassicornis*) 30,300 \pm 1,850 years B.P. to 11,910 \pm 180 years B.P.; wood bison (*Bison bison athabasca*) 1,350 \pm 95 years B.P.; Sargent's muskox (*Boötherium sargenti*) 25,540 \pm 900 years B.P.; helmeted muskox (*Symbos cavifrons*) >40,000 years B.P. to 17,695 \pm 445 years B.P.; tundra muskox (*Ovibos moschatus*) 2,830 \pm 100 years B.P.; Dall sheep (*Ovis ?dalli*) 23,000 \pm 600 years B.P. Except for the Alaskan bison, giant moose, large horse, and possibly the beaver, wapiti, wood bison and tundra muskox, on the basis of current radiocarbon dates, all of the preceding species can be considered to have occupied the Eastern Beringian refugium during the late Wisconsin glaciation.

8. An estimated 75% of the Yukon Pleistocene mammal species were derived from Eurasia or Beringia. Major influxes of Eurasian or western Beringian mammals entered Alaska and the Yukon via the Bering Isthmus - particularly during the Kansan and Illinoian glaciations. Many of them reached southern North America (e.g. *Bison*, *Alces*, *Panthera leo atrox*, *Mustela (Putorius) eversmanni*), while some did not (e.g. *Praeovibos*). The remaining 25% seem to have been derived from southern North America. Of these, I think the following species probably entered during an interglacial phase of the late Pleistocene - possibly mainly during the Sangamon: *Megalonyx* cf. *jeffersoni*, *Castoroides ohioensis*, *Ondatra zibethicus*, *Arctodus simus yukonensis*, *Taxidea taxus*,

Spilogale sp., *Mammut americanum*, *Equus* cf. *scotti* and *Camelops hesternus*. Their probable habitat requirements indicate that the route taken from southern North America to Eastern Beringia was dominated by dry scrub grassland, with occasional patches of spruce. Perhaps the muskrat and giant beaver moved northward along chains of lakes which formed as the Illinoian ice sheet melted back. Fossils of *Megalonyx* from central British Columbia and the Northwest Territories suggest that these ground sloths could have reached the Yukon through the central Cordillera or by the "western corridor" along the eastern flank of the Rocky Mountains. Remains of *Arctodus simus*, *Equus scotti*, *Camelops hesternus*, *Ondatra zibethicus*, and *Taxidea taxus* from deposits of probable Sangamon interglacial age at Fort Qu'Appelle and Saskatoon, Saskatchewan and Medicine Hat, Alberta, suggest that those species spread northward along the "western corridor". Discovery of one or two stratified Pleistocene mammal localities in the Peace River or Liard River regions would help to clarify this problem, and joint paleontological-archeological reconnaissances should be carried out there.

9. Based on evidence concerning habitat, albeit sparse in some cases, for 52 species of Yukon Pleistocene mammals described in this study, I estimate their ecological preferences as follows: grassland (30%), tundra (20%), forest (17%), water (11%), alpine terrain (3%). The dominance

of dry, cool grassland for long periods is clear, and is emphasized when the relative abundance of fossils representing bison, mammoth, horse and caribou are kept in mind. The number of species requiring moist, woodland habitat is surprisingly high considering the evidence for dryness throughout much of the late Pleistocene in central Alaska. This incidence is undoubtedly greatly influenced by the fact that most fossils were collected from the Old Crow Basin, which contained large glacial lakes during the latter half of the Pleistocene. Even during interglacials, such as the present one, there is much standing water in the basin.

10. Interesting glimpses of late Pleistocene paleoenvironments in the Old Crow Area have been gained as a result of careful collecting at two localities, followed by detailed analyses of samples by specialists in several disciplines. Unit 2 at Old Crow Locality 44 contains thick spruce logs and remains of smaller plants, molluscs, ostracodes, bryozoans, insects, fishes, birds and mammals. Many of the species suggest the former presence of ephemeral shallow ponds and lakes in a river flood plain with sandy margins and patches of forest in places. Ostracode remains and abundant small pond snail shells indicate shallow or quiet water with nearby vegetation. Fish, goose, duck, muskrat, beaver and giant beaver fossils support this view of the

past environment. Analyses of pollen samples from Unit 2 show high values for spruce, birch, sedges and grasses. Remains of a plant, *Najas flexilis*, and a spotted skunk (*Spilogale* sp.) suggest that climate was warmer than at present during at least part of the depositional episode concerned. I think that the fossils are of Sangamon interglacial age. A radiocarbon date on a spruce log from the unit is >54,000 years B.P.

Mollusc shells from Unit 4 at Porcupine Locality 100 yielded a radiocarbon date of $32,400 \pm 770$ years B.P. - a mid-Wisconsin age. Remains of plants, molluscs, ostracodes, bryozoans, crustaceans, insects, fishes (grayling) and mammals (brown lemming) demonstrate the former presence of a large, cool, shallow lake with a mud bottom, and with *Potamogeton* and wet meadow habitat near its margin. Coniferous trees, sedges, buttercups and cinquefoils grew nearby. Fossils representing large numbers of tundra-adapted insects and plants from Unit 4 suggest that tundra was located near the site, that the elevation of the tree-line in mid-Wisconsin time was lower and that climate was colder than at present. Probably open areas in this parkland type of environment were richer in grasses than in contemporary forest-tundra areas.

It is interesting to speculate on the causes and repercussions of changing environments in Eastern Beringia

toward the close of the late Wisconsin glaciation. The Bering Strait reopened then, and I postulate that easterly-moving storm tracks altered radically as a result, the new storms having their sources farther north in the Bering Strait, producing warmer, wetter conditions in Alaska and the Yukon. Consequently, cool, dry grasslands gave way to expanding spruce forests and boggy terrain there. Could such striking changes in vegetation have contributed substantially to the demise of large-horned bison (*Bison crassicornis* - apparently adapted to cool, dry grasslands), and the rise of western bison (*Bison bison occidentalis* - apparently adapted to moister, more heavily wooded habitat) about 12,000 years ago? Could other Pleistocene mammals that evidently flourished in Eastern Beringia during the late Wisconsin, such as woolly mammoths and Yukon wild asses, have succumbed because of the rapidity of such environmental changes at this critical period? Many problems like these await study.

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APPENDIX I Staining of Quaternary bones from the
northern Yukon Territory in relation to
geological age.

In 1974, in co-operation with R. Bonnichsen, 22 samples of dated mammal bone from the Old Crow Area were submitted to P. Tymchuk (Division of Chemistry, National Research Council) for bone mineral analysis using the emission spectroscopy technique.* The first group of three samples included moose (*Alces alces*), and caribou (*Rangifer tarandus*) bones that dated from approximately 80 years B.P. to 2,000 years B.P. This sample was whitish to pale tan in surface staining. The second group of 11 samples included wapiti (*Cervus elaphus*), and large-horned bison (*Bison crassicornis*) bones that had been radiocarbon dated between $4,570 \pm 100$ years B.P. and $12,460 \pm 220$ years B.P. by Teledyne Isotopes. This sample was manila to dark tan in surface staining. The third group of eight samples included mammoth (*Mammuthus* sp.), large-horned bison (*Bison crassicornis*), giant moose (*Alces latifrons*) and large horse (*Equus* sp.) that had been radiocarbon dated between $33,800 \pm 200$ years B.P. and $>39,900$ years B.P. These bones were chocolate brown to black in their surface staining.

As expected, iron and manganese were important in

* Readings indicate the per cent concentration of each element in the sample.

differentiating geologically younger from older bone. Obviously these two elements in the groundwater had been largely responsible for the brown to black staining of the older bones. However, among the suite of 23 elements recorded in this instance by the emission spectroscopy method (Sr, Co, Ni, Na, Zn, Ag, Cu, Zr, Ti, Al, Ca, V, Fe, Si, Pb, Mn, Mg, B, Ba, Yb, Y, and Au), two rarer elements, barium and strontium, appeared to have some value in differentiating younger from older bone.

In the first group, dating between approximately 80 years B.P. and 2,000 years B.P., iron readings ranged from 0.1 to 0.3, whereas the second group, dating between approximately 4,500 years B.P. and 12,500 years B.P., and the third group dating more than 33,800 years B.P., yielded readings between 3.0 and 5.0 (except for one reading of 0.1 from the centre of Sample 2), and 5.0 to 6.0, respectively.

Manganese from bone of the first group yielded readings of 0.005 to 0.1, whereas the second and third groups gave readings between 0.05 and 0.3 (except for one reading of 0.001 from the centre of Sample 2), and 0.1 to 0.25, respectively.

Barium from bone of the first group gave readings of 0.03 to 0.04, whereas the second and third groups yielded

readings between 0.03 and 0.3 (except for one reading of 0.01 from the centre of Sample 2), and 0.1 to 0.3, respectively.

Strontium from bone of the first group gave readings of 0.01, whereas the second and third groups yielded readings between 0.01 and 0.03, and 0.02 and 0.05, respectively.

These limited data indicate that whitish to tan bone of postglacial and late Wisconsin age can usually be separated from the chocolate brown to black bone of pre-late Wisconsin age (i.e. >33,800 years B.P.). The analysis also indicates that such elements as iron and manganese are particularly important in bringing about the darker staining of older bone, a point that I became aware of in 1968 after I had received the first radiocarbon date of $12,460 \pm 220$ years B.P. on fresh-looking bison bone from Old Crow Locality 11(1). The concentration of iron, manganese, barium and strontium seems to increase in direct proportion to the increase in age of the bones. Furthermore, the analysis suggests that iron, manganese, barium and probably many other elements, decrease in concentration from the outer surface of the bone to a point near the centre (e.g. Sample 2). This is apparent when looking at sections through many Pleistocene bones - generally they are darker

near the surface and lighter near the centre. Presumably the elements are concentrated at varying rates during periods of active groundwater. In 1968, I hypothesized that the darkest bones had undergone penetration by iron and manganese during the mid-Wisconsin interstadial or Sangamon interglacial, because groundwater carrying the minerals was probably most active during these phases. Presumably, also, most of the bones of mammals that had died in the Dawson and Old Crow areas between approximately 30,000 years B.P. and 12,000 years B.P. had been preserved in permafrost for most of the time until they were exposed and collected. Thus, there would have been little opportunity for penetration of the bones by minerals in the groundwater, and this would explain their relatively fresh appearance.

It should be kept in mind that these are only preliminary results, and that the subject requires much more detailed investigation.

An apparent exception to this bone-staining hypothesis is a horncore of an Alaskan bison (*Bison alaskensis*, NMC 13506 from Dawson Locality 33; Figure 76) that yielded a radiocarbon date of >39,900 years B.P. It is not much darker than most *Bison crassicornis* horncores from the Yukon dating between approximately 30,000 years B.P. and 20,000 years B.P., except for a black area on the dorsal surface.

A few specimens display an unusual combination of darkly-stained cranial bone and unusually white, fresh-looking teeth (e.g. a wolverine (*Gulo gulo*) cranium (NMC 14582 from the bar opposite Old Crow Locality 22; Figure 41) and a red fox (*Vulpes vulpes*) cranium (NMC 14353 from Old Crow Locality 115; Figure 31)). They are tentatively considered to be of Pleistocene or postglacial age.

APPENDIX II Criteria used for suggesting the geological age of Yukon Pleistocene mammal fossils.

Species	Suggested Age	Criteria			
		Radiocarbon Dating (years B.P.)	Stratigraphic Position	Staining of Bone	Evolutionary Stage
<i>Planisorex cf. dixonensis</i>	early Pleistocene (?Nebraskan)	_____	Nebraskan, in southern N. America	pre-late Wisconsin	_____
<i>Bomo sp.</i>	late Pleistocene	27,000 \pm 3000 -2000 date on bone artifact	_____	pre-late Wisconsin and ?late Wisconsin	_____
<i>Megalonyx cf. jeffersoni</i>	pre-late Wisconsin (?Sangamon)	_____	_____	pre-late Wisconsin	?pre-Wisconsin
<i>Ochotona cf. whartoni</i>	early Pleistocene (?Nebraskan)	_____	?Nebraskan, in Alaska	pre-late Wisconsin	_____
<i>Ochotona princeps</i>	pre-late Wisconsin (?Sangamon)	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	_____
<i>Lepus americanus</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Lepus arcticus</i>	pre-late Wisconsin (?Sangamon)	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	_____
<i>Marmota cf. monax</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Spermophilus parryi</i>	?Sangamon to late Wisconsin	>54,000, indirect date on wood	?Sangamon, late Wisconsin	pre-late Wisconsin, late Wisconsin	_____
<i>Castor canadensis</i>	?Sangamon to late Wisconsin	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin, late Wisconsin	_____
<i>Castoroides ohioensis</i>	?Sangamon	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	_____
<i>Dicrostonyx cf. henseli</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Dicrostonyx torquatus</i>	?Sangamon to late Wisconsin	>54,000, indirect date on wood	?Sangamon, late Wisconsin	pre-late Wisconsin, late Wisconsin	_____
<i>Lemmus sibiricus</i>	?Sangamon to mid-Wisconsin	32,400 \pm 770, >54,000, indirect date on wood	?Sangamon, mid-Wisconsin	pre-late Wisconsin	_____
<i>Clethrionomys cf. rutilus</i>	?Sangamon	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	_____
<i>Ondatra sibethicus</i>	?Sangamon	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	small size of M ₁ s suggests Sangamon
<i>Microtus (Stenocranius) miurus</i>	?Sangamon	_____	?Sangamon	pre-late Wisconsin	_____
<i>Microtus xanthognathus</i>	?Sangamon	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	_____
Order Cetacea, genus and species indeterminate	Sangamon or earlier	_____	pre-early Wisconsin	pre-late Wisconsin	_____
<i>Canis lupus</i>	?Sangamon to late Wisconsin	>54,000, indirect date on wood	?Sangamon, late Wisconsin	pre-late Wisconsin, late Wisconsin	_____
<i>Canis familiaris</i>	pre-late Wisconsin to postglacial	_____	probably late Wisconsin	pre-late Wisconsin, late Wisconsin or postglacial	_____

APPENDIX II... (cont'd.)

Species	Suggested Age	Criteria			
		Radiocarbon Dating (years B.P.)	Stratigraphic Position	Staining of Bone	Evolutionary Stage
<i>Alopex lagopus</i>	?Sangamon to late Wisconsin	>54,000, indirect date on wood	?Sangamon, late Wisconsin	pre-late Wisconsin, late Wisconsin	_____
<i>Vulpes vulpes</i>	pre-late Wisconsin to postglacial	_____	_____	pre-late Wisconsin (cranial bone) to postglacial (teeth)	_____
<i>Cuon</i> sp.	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Arctodus simus</i> <i>yukonensis</i>	pre-late Wisconsin (?Sangamon) to ?late Wisconsin	_____	_____	pre-late Wisconsin, ?late Wisconsin	_____
<i>Ursus</i> cf. <i>americanus</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Ursus arctos</i>	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Mustela erminea</i>	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Mustela (Putorius)</i> <i>eversmanni</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Martes nobilis</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Martes pennanti</i>	pre-late Wisconsin (?Sangamon)	_____	_____	pre-late Wisconsin	_____
<i>Gulo gulo</i>	?Sangamon to postglacial	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin (cranial bone) to postglacial (teeth)	small size of teeth may indicate an interglacial (?Sangamon)
<i>Taxidea taxus</i>	late Wisconsin	_____	_____	late Wisconsin	_____
<i>Spilogale</i> sp.	?Sangamon	>54,000, indirect date on wood	?Sangamon	pre-late Wisconsin	_____
<i>Lontra canadensis</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Felis (Lynx)</i> <i>canadensis</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Felis (Puma)</i> cf. <i>concolor</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Panthera leo atrox</i>	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Homotherium serum</i>	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Phoca</i> cf. (<i>Pusa</i>) <i> hispida</i>	?Sangamon	_____	?Sangamon	pre-late Wisconsin	_____
<i>Mammut americanum</i>	pre-late Wisconsin (possibly Sangamon)	?>54,000, indirect date on wood	possibly Sangamon, but not definitely in place	pre-late Wisconsin	_____

APPENDIX II... (cont'd.)

Species	Suggested Age	Criteria			
		Radiocarbon Dating (years B.P.)	Stratigraphic Position	Staining of Bone	Evolutionary Stage
<i>Mammuthus meridionalis</i>	early Pleistocene	_____	_____	pre-late Wisconsin	early Pleistocene in Eurasia
<i>Mammuthus</i> cf. <i>armeniae</i>	middle to late Pleistocene	_____	_____	pre-late Wisconsin, late Wisconsin	middle to late Pleistocene
<i>Mammuthus primigenius</i>	late Pleistocene (Wisconsin)	probably from >39,900 to 16,000 \pm 130; Whitestone mammoth is 30,300 \pm 2000	_____	pre-late Wisconsin, late Wisconsin	Wisconsin
<i>Equus</i> cf. (<i>Plesippus</i>) <i>verae</i>	middle to late Pleistocene (late Wisconsin)	dates of >39,900 and 34,000 \pm 2600 probably apply to this species	?Illinoian, ?Sangamon	pre-late Wisconsin, late Wisconsin	middle Pleistocene in Eurasia
<i>Equus</i> sp.	?middle Pleistocene	_____	_____	pre-late Wisconsin	?middle Pleistocene
<i>Equus</i> cf. <i>scotti</i>	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Equus (Asinus) lambert</i>	pre-late Wisconsin to late Wisconsin	14,870 \pm 260	late Wisconsin	pre-late Wisconsin, late Wisconsin	_____
<i>Equus (Asinus)</i> cf. <i>kiang</i>	late Wisconsin	_____	late Wisconsin	late Wisconsin	_____
Camelini (genus and species indeterminate)	?middle to late Pleistocene	>54,000, indirect date on wood	late ?Illinoian or early ?Sangamon	pre-late Wisconsin	_____
<i>Camelops hesternus</i>	late Wisconsin	_____	_____	late Wisconsin	_____
<i>Cervus elaphus</i>	late Wisconsin to postglacial	4,570 \pm 100	_____	late Wisconsin, postglacial	_____
<i>Alces latifrons</i>	?middle to late Pleistocene (mid-Wisconsin)	33,800 \pm 2000	_____	pre-late Wisconsin	middle Pleistocene in Eurasia
<i>Alces alces</i>	late Pleistocene (Wisconsin)	_____	_____	pre-late Wisconsin, late Wisconsin	late Pleistocene
<i>Rangifer tarandus</i>	?Illinoian to postglacial	27,000 \pm 3000 to 5,010 \pm 100	?Illinoian to postglacial	pre-late Wisconsin, late Wisconsin, postglacial	_____
Cervidae (genera and species undetermined)					
First group	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
Second group	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Bison alaskensis</i>	?middle Pleistocene (pre-late Wisconsin)	>39,900	?pre-late Wisconsin	looks like late Wisconsin, except for dark stain on dorsal surface of horncore	middle Pleistocene in Eurasia
<i>Bison crassicornis</i>	mid-Wisconsin to late Wisconsin	33,800 \pm 2000 to 11,910 \pm 180	late Wisconsin	late Wisconsin	?late Pleistocene
<i>Bison bison</i> <i>occidentalis</i>	late Wisconsin	_____	_____	late Wisconsin	late Wisconsin to early postglacial

APPENDIX II... (cont'd.)

Species	Suggested Age	Criteria			
		Radiocarbon Dating (years B.P.)	Stratigraphic Position	Staining of Bone	Evolutionary Stage
<i>Bison bison</i> <i>athabascas</i>	late postglacial	1,350 ± 95	postglacial	postglacial	late postglacial
<i>Soergelia</i> cf. <i>elisabethae</i>	middle Pleistocene (Kansan)	_____	_____	pre-late Wisconsin	middle Pleistocene (Kansan)
<i>Bootherium</i> <i>sargenti</i>	pre-late Wisconsin	_____	_____	pre-late Wisconsin	_____
<i>Symbos cavifrons</i>	pre-late Wisconsin to late Wisconsin	_____	_____	pre-late Wisconsin, late Wisconsin	_____
<i>Pracovibos priscus</i>	?middle Pleistocene; possibly Illinoian	_____	_____	pre-late Wisconsin	middle Pleistocene in Eurasia; Illinoian in Alaska
<i>Ovibos moschatus</i>	?late Pleistocene (pre-late Wisconsin to late Wisconsin) to postglacial	2,830 ± 600	postglacial	pre-late Wisconsin, late Wisconsin, postglacial	mainly late Pleistocene
<i>Ovis dalli</i>	late Wisconsin	23,000 ± 600	late Wisconsin	late Wisconsin	_____

B30194